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TAXONOMIC AND GENETIC RELATIONSHIPS OF EASTERN NORTH AMERICAN SPECIES OF ELYMUS WITH SETACEOUS GLUMES[1]

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In the grass genus *Elymus*, the origin of populations that exhibit varying degrees of reduction in glume structure is considered to have occurred frequently through natural hybridity between *Elymus Hystrix* L. (*Hystrix patula* Moench) and other sympatric species. Although spikes of *E. Hystrix* usually are recognized by the absence of glumes or the presence of reduced stubs, individuals showing occasional bristle-like glumes are not uncommon (fig. 17). Moreover, Great Lakes populations may be encountered that consist of spikes with the usual divergent spikelets and also the unusual development of long, filamentous or setaceous pairs of glumes at each rachis node (fig. 25 center). Such populations might have arisen through natural crosses between typical glumeless *E. Hystrix* and some other species with well developed glumes.

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Growing sympatrically with these variable populations are some well-established species, previously unrecognized in the Great Lakes area; i.e., *E. diversiglumis* Scribn. & Ball and *E. Wiegandii* Fern. Both of these species may have narrow or setaceous glumes and together with the sympatric *E. canadensis* L. var. *canadensis* they have been regarded as being involved in natural hybrid species complexes with *E. Hystrix.*

The first part of this treatise deals with taxonomic reassessments of these species. The second part is a report of experiments in interspecific hybridization that have been useful in interpreting the degree of genetic barriers existing between the species concerned, as well as in indicating patterns of natural hybridity by which new taxa might originate. A second paper records the currently active process of speciation involving *E. Hystrix* and components of *E. virginicus* L. in the Pine Hills area of southern Illinois.

All the known species of eastern American *Elymus* are tetraploid ($2N = 28$) and apparently differ only slightly in genomic structure. It has been demonstrated in previous studies that such usually diverse and widespread species as *E. canadensis* var. *canadensis* and *E. virginicus* var. *virginicus* will hybridize freely even though the F_1 is sterile (Church 1954, 1959). Partly fertile populations, intermediate between these species, have been reported to have arisen through introgressive hybridization in Iowa (Pohl 1959) and Texas (Brown and Pratt 1960).

Still further evidence of genetic fluidity in the Hordeae tribe, of which *Elymus* is a member, is presented in the many cases of intergeneric hybrids, both artificial and natural; i.e., *Elymus* and *Hordeum* (Bowden 1958, Pohl 1966), *Elymus* and *Sitanion* (Stebbins et al 1954), *Elymus* and *Agropyron* (Stebbins 1956 and Dewey 1966), *Agropyron* and *Hordeum* (Gross 1960), and *Agropyron* and *Sitanion* (Boyle 1963 and Dewey 1964). As far as is known to the author, the only report of a probable natural hybrid involving *Hystrix* is that with *Agropyron* reported by Dore (1950). There is an adequate basis, then, for suspecting that *E. Hystrix (Hystrix patula)* has played a role in either the interspecific or intergeneric hybrid origin of new taxa — a hypothesis that provides a large part of the framework for the present studies.

TAXONOMIC RELATIONSHIPS

1. *Elymus diversiglumis* Scribn. & Ball

In their study of *Elymus* in Minnesota, Booher and Tryon (1948) suggested the hypothesis that populations in the area of "E. interruptus" with reduced glumes might well be a product of hybridity of *E. canadensis* var. *canadensis* and *Hystrix patula.*

In a later paper deading with *Elymus* (Church 1954), preliminary studies indicated that the commonly recognized *E. interruptus* of the Great Lakes region of North America is a very different taxon from *E. interruptus* Buckley of Texas (1862), contrary to treatments in current manuals (Hitchcock and Chase 1950, Fernald 1950, Stevens 1950, Gleason 1952, Frazer and Russell 1954, Scoggan 1957). Wiegand (1918) in his study of eastern North American *Elymus,* however, clearly understood *E. diversiglumis* Scribn. & Ball as the species with subulate, unequal glumes in the northern Great Plains. Rydberg (1922) likewise recognized *E. diversiglumis* in his *Flora of the Rocky Mountains and Adjacent Plains.* Bowden (1964), in conference with the present author, also recognizes *E. diversiglumis* in his extensive treatment of *Elymus* in Canada. It will be demonstrated here that the misunderstood "interruptus complexes" of the central United States and adjacent Canada undoubtedly are composed of *E. diversiglumis* and of occasional introgressants of this species with *E. canadensis* var. *canadensis.*

The original description of *E. diversiglumis* published by Scribner and Ball (1901) is clear in stating that the "empty glumes are subulate — varying from a mere point to 1.5 cm in the same spikelet." The unequal pairs of subulate glumes that are so characteristic of specimens from central Minnesota (figs. 2 left, 5) are readily matched by those in the TYPE specimens from Crook County in northeastern Wyoming. *Elymus diversiglumis* is particularly abundant along clearings and road-cuts in the oak-aspen forests of the Itasca Park region of central Minnesota where it flourishes in company with *E. canadensis* var. *canadensis.* It may be distinguished in late July by well-seeded, deeply arched and silvery-hirsute spikes that have matured two to four weeks in advance of those of var. *canadensis* (figs. 9 vs. 11).

In searching for additional distinguishing features for *E. diversiglumis,* it has been noted that specimens from any part of the range indicated in the list of citations always possess a palea with an obtuse apex, usually augmented by a median tuft of hairs — quite in contrast to the acute, denticulate or retuse palea apices of *E. canadensis* var. *canadensis,* as indicated in the key to species. The two taxa are similar in exhibiting 6 or 7 nodes and leaves 6-10 mm in width. With very few exceptions, however, the distinct pilosity of the upper surface of *diversiglumis* leaves separates them from those of var. *canadensis.* When populations are encountered with the glumes falling below 0.8 mm in width and the striations not continuing clearly to the base, hybridity between the two taxa may be suspected.

The fact that *diversiglumis* and var. *canadensis* may hybridize to give rise to sterile F_1 offspring that in turn may produce fertile backcrosses to var. *canadensis* has been demonstrated by the author (Church 1959) and is more fully documented below. Such fertile introgressants and sterile, integrading forms appear occasionally, as might be expected, in disturbed areas.

Populations selected for study were distributed in woodland areas adjacent to, or within a few miles of, the following lakes in central Minnesota: — McCraney, Itasca, Gull, Long, Round and Mille Lacs. Along the disturbed aspen and oak woodland of the La Salle Trail and new Route 92 through Itasca Park in Hubbard County, for example, abundant stands of *E. diversiglumis* are established. Most specimens appear like those in figs. 5, 9 and 2 (left) which breed true from seeds grown in the greenhouse. An infrequent sample (2340)[2] may give rise to forms with wider glumes approaching those of *E. canadensis* var. *canadensis* figs. 6, 11) with which it is a common associate. Still other forms (2327) have paleas as long as those in var. *canadensis* (9.5 mm) and narrow but striated glumes equal in length (22 mm). This intermediate form is quite sterile. Even some typical *diversiglumis* forms (2328) may be at least 50% sterile. On the other hand, on a stretch of gravel roadside west from Itasca Park to McCraney Lake (Route 113), sympatric populations of *E. diversiglumis, E. canadensis* var. *canadensis* and *E. Hystrix* were remarkably distinct. However, on an extensively cut *Tilia* woodland near the shore of McCraney Lake, an unusually tall, vigorous and aggressive stand of *E. diversiglumis* (2461) was encountered. Although it possessed the usual spikelet characters of *E. diversiglumis* (cf. key), its wide leaves and strongly drooping spikes simulated these features of *E. Wiegandii.* Seed grown descendants maintain the same vigor in outdoor plots in Providence.

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[2] Citations in the text refer to the author's specimens on file in the Brown University Herbarium.

Again, a disturbed terrain has facilitated the spread of apparent hybrid forms (2514) of *E. diversiglumis* in the extensively bulldozed woodland roads adjacent to Gull Lake in Crow Wing County. The plants have glumes approaching those of var. *canadensis* in appearance, high percentages of shrivelled pollen and low seed set.

In spite of the above instances of apparent interspecific hybridity in Minnesota, on an isolated bluff, Elk Mound (Dunn County) in western Wisconsin, the undisturbed woodland glades harbor both taxa, morphologically distinct, in closely adjacent sites.

Further support for the integrity of *E. diversiglumis* has been presented by Frère Jean-Paul Bernard (of the Institution des Sourds-Muets, Montreal) who has made careful studies of *Elymus* in the Otterburne region of Manitoba, and to whom the author is greatly indebted for sending an unpublished manuscript (1958). Frère Bernard tested the hypothesis that *E. diversiglumis* might be a shade adapted form of *E. canadensis* var. *canadensis* by studying transplants of the former species to open, exposed habitats. No changes in morphological features were noted. Likewise, the present author, in the course of genetical studies, has observed only increased vigor of growth of typical representatives of *E. diversiglumis* transferred to open field plots. The importance of field observations is further emphasized by Frère Bernard who states, "Sur le terrain, la pubescence des lemmas parait blanche soyeuse à première vue chez l'*E. diversiglumis*, tandis qu'elle est plutôt terne chez l'*E. canadensis* (toutefois, cette distinction s'efface plus ou moins durant le séchage de spécimens)." Bernard also notes the aggressiveness of this species: "l'auteur a observé des touffes de cette espèce à glumes sétacées croissant en bordure d'un chemin traversant un secteur déboisé depuis quelques années."

In recognition of the appropriateness of the Scribner and Ball designation for the taxon with unequal glumes found in the Great Lakes region and with scattered stations westward to Wyoming and Saskatchewan, the following modification and expansion of the original description is presented:

Elymus diversiglumis Scribner & Ball (U.S.D.A. Bull. Agrost. **24**: 48-49. Fig. 22. 1901.). TYPE: *T. A. Williams 2653* (US!), Wyoming, Crook County, Bear Lodge Mountains, rich, open woods at 6000 feet.

CULMS robust (70) 120 (160) cm high, glabrous; LEAVES 5-15 mm wide, usually pilose above (rarely, slightly scabrous), sheaths overlapping except in the tallest specimens; SPIKES flexuous and broadly to deeply arched at maturity, (8) 15 (24) cm long; RACHIS flattened, margins ciliate, internodes (3) 5-6 (10) mm long; SPIKELETS usually two per node and containing 2-3 florets and frequently an additional, terminal sterile floret; GLUMES 2-15 (20) mm long, 0.1-0.5 mm wide, very unequal in length, sometimes lacking, setaceous from an indurated base; LEMMAS (7) 9 (12) mm long, silvery hirsute, rarely hirtellous, the awn 2-3 times the length of the body and widely divergent at maturity; PALEA (8) 8.5 (9) mm long, slightly shorter than the lemma, the apex obtuse, usually with a small, median, spatulate projection covered with a tuft of hairs denser than those of the body; STAMENS (2) 2.5 (3.5) mm long.

Range: borders of mixed woodlands, clearings and disturbed areas, including river terraces; frequent in Minnesota with scattered stations in Wisconsin, Iowa, Ontario, Manitoba, Saskatchewan, North Dakota and eastern Wyoming.

SPECIMENS EXAMINED: SASKATCHEWAN: Saskatoon, *Macoun & Herriot 42962* (CU, SASK), *Fraser 12-77* (SASK); Assiniboia, Oxbow, *Dore*

& *Boivin 13324* (DAO); Montagne a l'Original, *Boivin 8362* (DAO). MANITOBA: Turtle Mountain, *Burgess 2229* (DAO); Beauséjour, *Dore 12800* (DAO); Indian Reserve, Prairie Meadow, *A. & D. Löve 6229* (DAO, MT); Riding Mountain Park, *Rowe 416, Halliday 32-157* (CAN, DAO), *Lovaas 61-27* (DAO); Otterburne, *Bernard 50-132, 54-572, 58-441, 536, 568, 607* (MT); Kleefeld, *Bernard 56-5422, 58-617* (MT); Stuartburn, *Bernard 58-568* (MT.); Clear Lake, *Halliday 157-1932* (CAN). ONTARIO: Rainy River District, *Dore 9118* (CAN, DAO); Thunder Bay District, *Lindsay 1251* (DAO). WYOMING: Crook County, *Williams 2653* TYPE, *2679* (US), NORTH DAKOTA: Dunn County, *Swallen 5799* (US), *Stevens & Moir* (NDA); Bottineau County, *Brannon 85150* (US), *Stevens 2512* (NDA); Pembina County, *Bergman* (MIN), *Stockbridge 974* (NDA); Cavalier County, *Stevens* (NDA). MINNESOTA: Beltrami County, *275174* (MIN); Clearwater County, *277388* (MIN), *Moore & Huff 18986* (DAO-MIN), *Church 2310-16, 2435* (BRU); Polk County, *64722, 64724* (MIN); Mahnomen County, *Church 2461* (BRU); Hubbard County, *Grant 2914* (IND, MO, MIN, NY), *2714* (MIN, US), *275776* (MIN), *Church 2328, 2340-47* (BRU); Becker County, *Grant 3901* (GH, MIN), *Church 2354-56, 2470, 2480* (BRU); Ottertail County, *371975* (MIN); Crow Wing County, *64727* (MIN), *Church 2360, 2506, 2512* (BRU); Stearns County, *64723* (MIN); Hennepin County, *Wheeler 1224* (GH, MIN, US); Scott County, *64726* (MIN). IOWA: Emmet County, *Wolden 530* (ISC). WISCONSIN: Bayfield County, *Weber* (WIS); Chippewa County, *Ebert* (WIS); Dunn County, *Myer 132* (WIS), *Church 2570* (BRU); Juneau County, *Truman* (WIS); Vilas County, *Stearns 570* (WIS); Polk County, *Baird* (WIS); Burnett County, *Shinners 4471* (WIS).

SPECIMENS INDICATING PROBABLE INTROGRESSION OF *E. diversiglumis* INTO *E. canadensis* var. *canadensis:* SOUTH DAKOTA: Lawrence County — *Martin 477* (US) — This specimen from Spearfish Canyon, roughly 25 miles from the TYPE locality in adjacent Wyoming, has rather thin, slightly pilose leaves and very narrow, setaceous glumes as in *E. diversiglumis.* The glumes are quite equal in length, however, and the 10.5 mm long paleas have acute, truncate or slightly concave apices — all of which features typify *canadensis* var. *canadensis.*

WYOMING: Crook County — Whereas the TYPE specimens, *Williams 2653* (US), from the Bear Lodge Mountains are easily matched by those from Welcome, *Williams 2679* (US), it is noteworthy that *Williams 2681* from the same "rich gulches" is nearer to *E. canadensis* var. *canadensis* in the bidentate apices of the paleas and the glabrous leaves. The collections of *Griffiths 925* and *942* (US) from Hulett are likewise regarded as forms of var. *canadensis* with setaceous glumes.

Elymus occidentalis Scribn. (1898) is a name cited by Hitchcock and Chase (1950) as a synonym for what is treated here as *E. diversiglumis.* Examination of the TYPE specimen, *Nelson 4470* (US) from

Albany County, Wyoming, reveals simply a dry river terrace form of *E. canadensis* var. *canadensis*.

2. *Elymus Wiegandii* Fern.

The description of *E. Wiegandii* published by Fernald (1933) makes quite clear the distinction between this species and *E. canadensis* var. *canadensis*. Hitchcock and Chase (1950), however, regard this species as one of many variants of *E. canadensis* var. *canadensis*. Bowden (1964) reduces *E. Wiegandii* to a variety of *E. canadensis*. On the other hand, Voss (unpublished) recognizes the specific distinctness of *E. Wiegandii* as it occurs sparingly in Michigan. Throughout its range, along shaded streams or alluvial river terraces, *E. Wiegandii* is readily identified by its lax spikes, hanging pendant from the time of emergence from the uppermost of the glaucous, usually overlapping leaf-sheaths (fig. 10). The culms are vigorous, bearing 9-12 leaves, 10-22 mm wide, dark green and frequently pilose on the upper surface. The glumes are usually less than 1 mm wide and the bases abruptly narrowed, indurated but not terete. Probably because of the fact that the glumes are frequently less than 0.5 mm wide, especially in populations in the Great Lakes area, the species has often been confused with *E. diversiglumis* or lumped under so-called *E. interruptus*.

Elymus Wiegandii may be distinguished at once from *E. diversiglumis* (cf. key) by the pendant, rather than deeply arched spikes (fig. 13) (a feature often obscured in mounted specimens), the usually wider and always greater number of leaves, the usually glabrous and overlapping leaf sheaths and the bidentate (rather than obtuse) dense-hairy apices of the paleas. The ranges of the two species overlap geographically in the broadest limits of the Great Lakes area, but *E. diversiglumis* is a plant of more open and drier terrain than the shaded, wet thickets of *E. Wiegandii*.

In the same areas of Minnesota that yielded so many stations for *E. diversiglumis* as well as *E. canadensis* var. *canadensis* and *E. Hystrix* (Itasca Park and Mille Lacs), several newly reported sympatric and ecologically distinct stands of *E. Wiegandii* are noteworthy as indicated in the following list: —

LAKE ITASCA: drainage in wet, coniferous woods, west of Park Road, — 2305; north boundary of Itasca Park, wet, mixed hemlock woods — 2438.

TULABY LAKE: drainage, mixed woods near Route 113 — 2493.

MILLE LACS LAKE: north of Garrison, shore road through mixed woodlands, wet, shady forest — 2517 (whole plant glaucous); north of Garrison, sandy, wet clearing under oaks — 2522; south of Vineland, shore road, mixed woodland — 2293-94, 2297-99, 2302.

ROUND LAKE: north of Brainerd, edges of sandy, wet, dense, mixed woods — 2500, 2502.

RICE LAKE: Lum Park, brook-dissected, oak-birch woods, near shore — 2499 (whole plant glaucous).

Likewise in New England and eastern Canada, the shaded, alluvial habitat of *E. Wiegandii* is in contrast to the more open and drier woodland-border habitat characteristic of *E. canadensis* var. *canadensis.* Pilosity of the adaxial leaf surfaces is a frequent but not too constant feature of *E. Wiegandii* in New England and Quebec as well as the midwest (Fassett 1951). Two populations collected by the author in closely adjacent stations in southwestern Wisconsin (Castle Rock Woods), illustrate the differences between superficially similar representatives of the two species. Both 2580 *(E. Wiegandii)* and 2579 *(E. canadensis* var. *canadensis)* are robust plants (ca. 120 cm tall) with pilose upper leaf surfaces, mostly overlapping sheaths, and paleas 10-12 mm long with bidenticulate apices. *E. Wiegandii,* however, has 10-12 nodes, leaves about 18-20 mm wide, sheaths glaucous, spikes pendant and glaucous, glumes ca. 17 mm long and 0.5 mm wide. This population (2580) grows on the edge of a shady, rich woodland resting on an abandoned alluvial terrace! In contrast, 2579 *(E. canadensis* var. *canadensis)* has 7-9 nodes, leaves 9-12 mm wide, the margins moderately inrolled, sheaths green, glumes 21-30 mm long and 0.8-1.0 mm wide. Although the habitat is within ca. 25 feet of a shady, alluvial thicket, the plants are confined to an open, dry roadside. Furthermore, the author has observed many other stations of *E. Wiegandii* in the field and invariably the habitat is a rich, alluvial soil in the shade. Although some forms of *E. canadensis* var. *canadensis* may be found on the moist lake shores of Lake Michigan, the contrasting habitat factors to those of *E. Wiegandii* are sand and full sunlight. On the whole, *E. Wiegandii* appears to be less capable of standing competition on open areas than either *E. canadensis* var. *canadensis* or *E. diversiglumis* and under greenhouse conditions it becomes quickly reduced in size much more than any other species of *Elymus* of this study.

The greatest concentration in the range of *E. Wiegandii* lies along the tributaries of the Connecticut and St. Lawrence Rivers, spreading out across New York and northern Pennsylvania and extending northward across northern New England to the Canadian Maritimes. More recently, several stations have been reported in the drainage systems of the Rainy, Mississippi, and Red Rivers in Ontario, Michigan, Wisconsin, and Minnesota with scattered stations westward in Iowa, the Dakotas, Wyoming and Manitoba. The most recently reported collections are from the banks of the rivers draining into James Bay on the Ontario side (Dutilly & Lepage 1963).

The following citations of specimens examined by the author indicate a much wider geographic range for *E. Wiegandii* than was known to Fernald in 1933: —

MANITOBA: Assiniboine, *Krivda* (DAO); Sans Souci, *Bernard 499, 5477* (MT); Otterburne, *Bernard 504, 525* (MT). ONTARIO: Rainy River County, *Dore 9175* (BRU, DAO); Thunder Bay County, *Garton 2063* (US), *Williamson 2239* (PENN); Carleton County, *Rolland 31* (US), *Dore 10, 541,* (BRU, DAO); Cochran County, *Dutilly & Lepage 36350, 36809, 38397* (LCU). QUEBEC: Champlain County, *Gagnon* (DAO); Huntington County, *Dore & Cody* (DAO), *Bassett & Frankton* (DAO); Pontiac County, *Dore 9028* (BRU, DAO); Brome County, *Dore 6* (GH); Vaudreuil County, *Ray 28420* (MT); Gatineau County, *Dore 15241* (DAO, MT), *Dore 5* (GH); St. Maurice County, *Stanislas 142* (MT); Stanislas County, *Marie-Victorin 7331* (MT); Richelieu County, *Marie-Victorin 6367* (MT); Portneuf County, *Marie-Victorin 45064* (GH, MT); Rimouski County, *Lepage 3260* (GH); Gaspe County, *Dore 47879* (US); Deux Montagne County, *Louis-Marie 2910* (US); Lac St. Jean County, *Kennedy 3* (GH); Terrebonne County, *Rolland-Ger-*

main 6061 (MT), *Rouleau 2528* (MT), Gray Ex. *1405* (GH, ISC), *Church 2528, 2532* (BRU); Bonaventure County, *Collins 5116* (GH), *Collins et. al.*, (GH, NY), *Rousseau 32528* (GH), *Marie-Victorin 32350, 33763, 48988* (DAO, GH), *Church 2533-36* (BRU), *Raymond 56069* (DAO); Sherbrook County, *Dore 345* (DAO); Drummond County, *Verret* (DAO). NOVA SCOTIA: Pictou County, *Smith 11677* (DAO, GH), *Erskine 53430* (DAO). NEW BRUNSWICK: Victoria County, *Marie-Victorin 46549* (GH, MT); Kings County, *Svenson & Fassett 3012* (GH); Madawaska County, *Dore 47951* (DAO). MAINE: Aroostock County, *Fernald 197* TYPE (GH), *Church 2537* (BRU); Piscatiquis County, *Parlin 1793* (GH), *Church 2538, 2540* (BRU); Kennebec County, *Fernald & Long 12748* (GH); Oxford County, *Parlin 2038* (GH); Somerset County, *Fernald & Long 490* (US). NEW HAMPSHIRE: Coos County, *Pease 10685* (GH), *Church 2376* (BRU); Grafton County, *Church 2226, 2231* (BRU); Sullivan County, *Cowden* (NEBC). VERMONT: Orleans County, *Church 2408* (BRU); Caledonia County, *Congdon* (GH); Bennington County, *Church 2210-12, 2217-19* (BRU); Rutland County, *Church 2263-64* (BRU), *Carpenter 3* (NEBC, US), *Kirk 1036* (US); Windham County *2214-16* (BRU), *Wheeler* (GH); Chittenden County, *Church 2250* (BRU), *James* (NY). MASSACHUSETTS: Hampden County, *Church 2526* (BRU); Hampshire County, *Church 2200-04* (BRU); Franklin County, *Church 2207* (BRU). CONNECTICUT: New Haven County, *Blewitt 35* (GH). NEW YORK: St. Lawrence County, *Phelps 134* (GH, NY); Washington County, *Dobbin & Burnham* (GH); Essex County, *House 25976* (GH); Columbia County, *McVaugh 2087* (PENN); Monroe County, *Hitchcock 16024* (US); Schoharie County, *Whitney 1844* (TEX); Tompkins County, *Wiegand 9295* (GH, NY, US); Madison County, *House 2860* (GH); Chemung County, *Axtell & Smith 2667* (CU, US); Onondago County, *Lippert 295* (SYR); Rensselaer County, *House 24015* (SYR); Oneida County, *1789* (SYR). PENNSYLVANIA: Warren County, *Wahl 9873* (GH, PENN); McKean County, *Fogg et. al. 19781* (PENN); Susquehanna County, *Glowenka 9399* (PENN); Wayne County, *Gress & Honesdale* (PENN); Wyoming County, *Glowenka 9281* (PENN). MICHIGAN: Houghton County, *Farwell 11607* (MICH); Chippewa County, *Dodge* (MICH); Oakland County, *Farwell 1556a* (MICH). WISCONSIN: Lincoln County, *Seymour 13129-30, 14464* (WIS), *Iwen 339* (WIS), *Church 2560* (BRU); Polk County, *Brenner* (WIS); Chippewa County, *Davis* (WIS); Eau Claire County, *Kunz 356* (WIS), *Fassett 22286-7* (WIS); Dane County, *Cheney* (WIS), *Hale* (WIS); Vernon County, *Iltis & Koeppen 11922* (WIS); Richland County, *Iltis & Koeppen 11841* (WIS); Grant County, *Fassett 28971-2, 26493* (WIS), *Church 2580, 2589* (BRU), *Iltis et. al. 13847* (WIS). MINNESOTA: Kittson County, *Moore 11604* (ISC, MIN); Cook County, *Butters & Abbe 1024* (GH, MIN); Beltrami County, *Pamel 72, 329* (ISC); Clearwater County, *Church 2305* (BRU); Carlton County, *Moore & Butters 3472* (GH, MIN); Becker County, *2438, 2493* (BRU); Crow Wing County, *Church 2499, 2517, 2522* (BRU); Aitkin County, *Church 2500* (BRU). IOWA: Dickinson County, *Thorne 13223* (ISC); Emmet County, *Wolden 566* (ISC). NORTH DAKOTA: Bottineau County, *Stevens* (NDA); Ward County, *Crosby* (NDA); Benson County, *Hitchcock 5064* (US), *Lunell 1020620* (US); Pembina County, *Stevens* (US); Barnes County, *Perrin 1346* (US), *Stevens & Moir* (US); Ransom County, *Stevens* (US); Cass County, *Stevens* (NDA), *Stevens 114* (DAO, NDA, US, WIS), *Bergman & Stevens* (NDA), *Stevens 1677* (GH); Sioux County, *Stevens 1559* (NDA, US). SOUTH DAKOTA: Roberts County, *Ball & Over 2224* (ISC), *Johnson 10* (GH, TEX). WYOMING: Crook County, *Ownbey 2377* (MIN, US), *Griffiths 925, 942* (US).

3. *Elymus canadensis* L.

a. var. *canadensis*

In central Minnesota, sympatric populations of var. *canadensis* and *E. diversiglumis* may occasionally give rise to variants with narrow glumes (ca. one half mm in width) that represent introgressants from the latter species. It has been noted further that *E. Wiegandii*, characterized by narrow glumes (cf. key), remains distinct from sympatric var. *canadensis*. In both cases, var. *canadensis* is distinguished by the stiff, glabrous leaves with involute margins, the erect or broadly arched spikes and the one mm wide glumes.

b. var. *brachystachys* (Scribn. & Ball) Farwell

Plants of this variety with compact spikes and glabrous lemmas were raised from seed collected in Llano County, Texas. They differed from the TYPE material *(Palmer 420* US!) in possessing glumes that were frequently approximately only one half mm in width. Since Scribner and Ball (1901) in their original description of this taxon had cited collections from Oklahoma to as far north as Michigan, it was thought by the author that *Elymus* populations with narrow glumes arising from hybridity with var. *brachystachys* might presently be encountered in the Great Lakes area. The search, particularly at the stations reported by Farwell (1920), proved to be unrewarding. However, since earlier collections of var. *brachystachys* from Texas had segregated for several variations in reduction of glume width (Church 1954), it appears that a process of speciation leading to varieties with narrow glumes might be occurring in the far South, involving a component of *E. canadensis*, but in an obviously distinctly different pattern from that which produces introgressants of *diversiglumis* into var. *canadensis* in Minnesota.

c. var. **interruptus** (Buckley) comb. nov. Based on *E. interruptus* Buckley, Acad. Nat. Sci. Phila. Proc. 1862:99. Llano County, Texas.

Since the name of this taxon has been misapplied to very different northern species with setaceous glumes, a revision of Buckley's original description is presented.

CULMS, slender, tufted 50-80 (100) cm high; LEAVES 15-20 cm long, 5-8 mm wide, scabrous and often glaucous; SHEATHS not exceeding nodes, margins usually ciliolate; SPIKE erect, (6) 8-15 cm long; RACHIS glabrous except for scabridulous margins; INTERVALS between spikelets on rachis (6) 8-14 mm long; GLUMES (15) 20 (30) mm long, equal, glabrous or scabridulous, base indurated and often terete, usually less than 0.5 mm wide at the middle of the body; SPIKELETS of 2, 3 or 4 florets with an additional, terminal, sterile floret; LEMMAS 8-9 mm long, glabrous and the awns 15-20 mm long, straight at maturity, margins scabridulous; PALEAS (7) 8 (9) mm long with the apices narrow, truncate and ciliolate. Rocky, open woodlands in Llano County, Texas.

The TYPE specimens collected by *Buckley* (PH!) consist of two culms about 60 cm high. The glumes are 20-22 mm long, 0.4-0.5 mm wide and the indurated bases have 2-3 nerves. The ISOTYPE (GH!) has even narrower, i.e., setaceous, glumes. Additional specimens from Llano County: *Wolf 3123* (US), *Smith* (US *1019698*), *Church and Brown 1041* (BRU), *Reverchon* (US *64974*).

Although var. *interruptus* appears to be restricted to Llano County, it is sympatric with var. *brachystachys* with which it shares a short (ca. 60 cm) stature and a time of floret maturity two months in advance of northern varieties growing in the same field plots in Providence. The two varieties are undoubtedly closely related, but they are distinguishable on morphological grounds (cf. figs. 3, 4, 7, 8). On the other hand, examination of figs. 9, 15, 1, and 2 will reveal the striking differences between var. *interruptus* and *diversiglumis* and clear the confusion that has existed between these taxa.

4. **Elymus Svensonii** sp. nov.

In searching records for further information concerning the range of both *E. diversiglumis* and *E. canadensis* var. *interruptus*, the case of the latter variety reported from an isolated station in Tennessee was noteworthy (Svenson 1941). Examination of the specimen on file in the Brooklyn Botanic Garden Herbarium revealed a plant quite distinct from either of the above taxa. Through the kindness of the collector, Dr. Henry K. Svenson, the author was able to find the exact area on the steep banks of the Cumberland River in Tennessee, the only station known in the state or elsewhere. The plants were scattered rather thickly in the edge of a high, limestone cliff woodland over a distance of not more than fifty feet. Although house-lots were laid in contact with the summit, the plants were spread down the river embankment, rather out of reach.

Since the population is unique in taxonomic features, it seems appropriate that it be described as a new species and named in honor of the original collector, Dr. Svenson.

Elymus Svensonii sp. nov. Planta tota glauca; 80-100 cm alta; culmo basi 2 mm lato; laminis 6-8 mm latis at 15-25 longis, supra minusve villosis, vaginis plerumque non excedentibus, auriculis rubidis — siccis fusco-brunneis; spicis erectis, arcuantibus, 12-16 cm longis, rachi applanato, sinuosissimo et segmentis racheos 8-12 mm longis; spiculis geminatis, in 3-4 floribus constantibus; glumis setosis, variatim 1-18 mm longis, plerumque mediostriatis, basi induratis subteretibus; geminis saepe in longitudine inaequalibus aut omnino deficientibus; lemmatibus 9-10 mm longis et aristis deinde valde curvatis 12-20 mm longis; palea 8-9 mm longa, apice lata, truncata aut parum convexa et margine breviter ciliata.

Entire plant glaucous; CULMS 80-100 cm high and the bases 2 mm in diameter; LEAVES 6-8 in number, 6-10 mm wide and 15-25 cm long, usually slightly villous above — the margins smooth or scabrellous; LEAF SHEATHS usually not overlapping and the auricles dark-red becoming reddish-brown on drying; SPIKE at first erect becoming broadly arched, 12-16 cm long; RACHIS, flattened, conspicuously sinuous, internodes 8-12 mm long, margins hirtellous; SPIKELETS, 2 at each node, composed of 4-5 florets and closely adpressed to the curves of the rachis internodes, florets not readily disarticulating from the pedicel joints; GLUMES, setiform usually with a median striation, indurated and nearly terete at the base, usually in unequal pairs 1-18 mm long, occasionally lacking; LEMMA 9-10 mm long, the widely divergent awn 12-20 mm long; PALEA 8-9 mm long, apex broad, truncate or slightly concave, margins villous; ANTHERS ca. 5 mm long; LODICULES asymmetrically bi-lobed, the larger lobe acute with margin ciliolate.

Known only from the TYPE locality: steep limestone bluffs on the Cumberland River at the end of an abandoned road off McGavock Pike and ca. 0.9 mile from the intersection with Lebanon Pike, just north of Donelson, Davidson Co., Tennessee.

HOLOTYPE: *Church 2527* (BRU) (figs. 12, 1 and 2). ISOTYPES: (GH, US). PARATYPES: *Svenson 9452* (BKL, MO).

Elymus Svensonii bears some resemblance to *E. Hystrix*, but differs from the latter species in exhibiting variable glumes, consistently arched rather than erect spikes, closely adpressed rather than divergent spikelets, usually a greater number of florets per spikelet, divergent rather than straight lemma awns (figs. 12, 1, 2).

Specimens in the United States National Herbarium collected by Gattinger in 1885 and labeled "precipices on the Cumberland Riv. near Nashville" (US 1021371) could, of course, have come from a station quite similar to that of *E. Svensonii. Asprella Hystrix* Willd. has been added to the label at some later date. The plants are not too well preserved, and probably represent *E. Hystrix* with vestigial glumes similar to another Gattinger collection (US 1021372) designated with no locality other than Nashville.

5. *Elymus Hystrix* L.
(Sp. Pl. 560. 1753, Virginia. Clayton.)

There is no more distinctive species in moist, shady wooded areas of the eastern United States than what has for a long time been recognized as *Hystrix patula* Moench. The widely spreading spikelets, falling quickly at maturity and the usual lack of glumes certainly appear to constitute sufficient bases for generic designation (fig. 17). Yet morphological variations of the common form are not unknown. For example, populations with pubescent lemmas have been designated as *H. patula* var. *Bigeloviana* (Fern.) Deam. Equally common are forms that exhibit occasional filiform glumes. Most striking of all are populations in which long, filiform glumes are found all along a rather sinuous rachis of rather closely compacted nodes (fig. 25). The latter variations are known throughout the range but are particularly frequent in the Carolinas as is indicated in the citations that follow.

SPECIMENS EXAMINED: NEW MEXICO: Colfax County, *Silveus 4928* (TEX). OKLAHOMA: Adair County, *Wallis 7606* (TEX). ARKANSAS; Petit Jean Mts., *Scully 974* (US); Baxter County, *Demaree 29337* (TEX); Randolph County, *Demaree 29190* (US); Sharp County, *Demaree 26890A* (US). MISSOURI: Jasper County, *Palmer 3781* (MO). ILLINOIS: Knox County, *Chase 1840* (US); Peoria County, *Chase 12053* (US). WISCONSIN: Burnett County, *Shinners 4475* (WIS); Calumet County, *Strandberg 376* (WIS); Dane County, *Cottam 184* (WIS); Grant County, *Iltis 13789* (WIS); Green County, *Struik* (WIS), *Fell 58438* (WIS); Lafayette County, *Coogan 149* (WIS); Rock County, *Fell 57938* (WIS); Sauk County, *Stowell* (WIS), *Church 2576* (BRU); Vernon County, *Iltis 6449* (WIS), *Marks* (WIS). INDIANA: Cass County, *Deam 25895* (US); Sullivan County, *Deam 25683* (US). OHIO: Coshocton County, *Moldencke 13124* (US). NOVA SCOTIA: Pictou County, *St. John 1387* (GH). MARYLAND: Prince Georges County, *Maxon 5988* (GH). WASHINGTON, D. C.: High Island, *Pollard 446* (US). VIRGINIA: Bedford County, *Curtiss* (GH); Culpepper County, *Allard 1787* (GH); Greensville County, *Fernald & Long 8029* (GH). NORTH CAROLINA: Alamance County, *Ramseur 2277* (DUKE), *Bell 4149* (DUKE); Anson County, *Radford 13146* (NCU); Davidson County, *Radford 12828, 7069* (NCU); Durham County, *Bloomquist 14526* (UNC), *793, 797* (DUKE); *Godfrey & Fox 51163* (DUKE, UNC); *Wilbur 6193* (DUKE, GH, US); Granville County, *Batson 334* (NCU), *Fox 4912* (DUKE); Haywood County, *Silveus & Bloomquist 9765* (TEX); Lee County, *Beard 1072* (NCU); Macon County, *Quaterman 1442* (DUKE); Orange County, *Bloomquist et. al. 402* (GH), *Radford & Stewart 681a, 212a* (NCU); Person County, *Bell 14652* (NCU); Rockingham County, *Radford 13639* (DUKE); Rowan County, *Horton 1407* (NCU); Stanley County, *Ahles 16222* (NCU); Union County, *Ahles 27513* (NCU); Wake County, *Boyce 1620* (NCU), *Godfrey 48127* (GH), *Brown 51207* (TEX). SOUTH CAROLINA: Abbeville County, *Radford 26037;* Chesterfield County, *Radford 12397* (DUKE, NCU); Edgefield County, *Radford 26361* (NCU); Kershaw County, *Radford 23669* (NCU); Lancaster County, *Ahles 31356* (NCU); McCormick County, *Radford 22327* (NCU); Newberry County, *Bell 9235* (NCU); Saluda County, *Radford 23123* (NCU).

The author has examined in the Linnean Herbarium in London the Savage indexed sheet 100.8 upon which the name *Elymus Hystrix* is based. Three specimens are rather young since the glabrous spikes are barely out of the terminal leaf sheaths. Leaves and sheaths are dark green and slightly pilose. Glumes are entirely lacking. The spike rachis is thin and straight with ciliolate margins and the internodal distances are ca. 5 mm. The straight awns are ca. 2½ times the length of the 10 mm long lemmas. Paleas are 9 mm long and the apices are acute and slightly notched.

Except for the fact that the Linnean specimens are immature and do not exhibit the spreading spikelets, they are quite similar to those selected over the wide eastern United States range. The many variations listed above, however, indicate rather strongly that they must be the product of some pattern of hybridity with other species of *Elymus*, perhaps arising pandemically in the eastern United States.

The experimental studies reported later will present a further basis for evaluating the phylogenetic position of *E. Hystrix* in the relationships of *Elymus* species. It will be demonstrated that employment of the original Linnean name (Bowden 1964) is quite justifiable on genetic as well as on morphological grounds.

Key to Eastern North American *Elymus**

1. Pairs of glumes mostly unequal in length, often setaceous, reduced to pointed stubs or lacking (if paleas 9-12 mm long and apices bidentate, cf. *E. Wiegandii)*
  2. Spikes erect at maturity; spikelets usually widely divergent from the rachis and readily falling when dry; glumes lacking or occasionally present as filiform bristles at some or all nodes; paleas 8 (9-10) mm long, apices obtuse or truncate, often pilose on the upper margin. .... *E. Hystrix.*
  2. Spikes slightly to broadly arched at maturity; spikelets more or less adpressed to the rachis; glumes setaceous, 0.1 mm-0.5 mm wide, tapering from an indurated base.
    3. Lemmas densely hirsute; paleas (7.5) 8 (9) mm long, apices obtuse with median tuft of hairs; upper leaf surface usually pilose; entire plant green otherwise. .... *E. diversiglumis.*
    3. Lemmas glabrous; paleas 8-9 mm long, apices narrow and truncate or retuse, cilolate; entire plant glaucous. .... *E. Svensonii.*
1. Pairs of glumes essentially equal in length.
  4. Spikes abruptly pendant on emergence from the leaf sheaths, the latter usually glaucous and overlapping; leaf blades commonly pilose above, 12-28 mm wide; glumes (0.2) 0.5 (1.2) mm

wide, often setaceous with base narrowed and indurated; paleas (9) 11 (12) mm long, apices bidentate. .... *E. Wiegandii.*

4. Spikes erect or becoming slightly to broadly arched at maturity.

5. Glume bases clearly indurated.

6. Glumes 0.8-2 mm wide, swollen on half or all of the adaxial surface as well as the abaxial base, sometimes bowed and disarticulating along with the spikelets in age; paleas 6-8 (8.5) mm long, apices obtuse, truncate or slightly emarginate; spikes erect. .... *E. virginicus.*

7. Glumes 1-2.7 cm long, spike at times partly included in sheath. .... var. *virginicus.*

7. Glumes 2.7-1.0 cm long, spike well exerted. .... var. *glabriflorus.*

8. Spikelets glabrous. .... f. *glabriflorus.*

8. Spikelets hirsute. .... f. *australis.*

6. Glumes 0.2-1.0 mm wide, indurated for 1-3 mm adaxially, striated middle area more or less convex.

9. Paleas 5.5-6.5 mm long, apices obtuse; rachis internodes 1.5-3.0 mm long, whole spike villous, lemmas rarely glabrescent. .... *E. villosus.*

9. Paleas (7) 8.5 (9) mm long.

10. Apices bidentate; rachis internodes (3) 4-5 (7) mm long; glumes scabrous to hispidulous. .... *E. riparius.*

10. Apices truncate or slightly retuse; rachis internodes (6) 8 (9) mm long; glumes 0.2-0.5 (0.6) mm wide; lemmas glabrous; leaf-sheath margins usually ciliate. .... *E. canadensis* var. *interruptus.*

5. Glume bases thin and striated or indurated for only 1.0 mm; body of glume not thickened adaxially.

11. Spikes (7) 10-20 (30) cm long broadly arched at maturity; spike internodes (4) 5 (7) mm long; paleas (8.5) 9-12 (14) mm long, apex very acute and usually bidentate; lemmas hirsute or hirtellous; glumes (0.7)-1.0 mm wide; maturity in July and August. .... *E. canadensis* var. *canadensis.*

12. Plants green. .... f. *canadensis.*

12. Plants glaucous. .... f. *glaucifolius.*

11. Spikes (7) 10-12 (15) cm long, essentially straight at maturity; spike internodes (2) 4 (5) mm long; paleas (7) 9-10 mm long, apex acute and truncate or bidenticulate; lemmas glabrous or scabrous; glumes 0.5-1.0 mm wide; maturity in late May and June. .... *E. canadensis* var. *brachystachys.*

*Leaf measurements are from the third leaf beneath the spike. Spikelet measurements are taken from the mid-spike area. Extremes of measurements are indicated in parentheses.

Plate 1342.

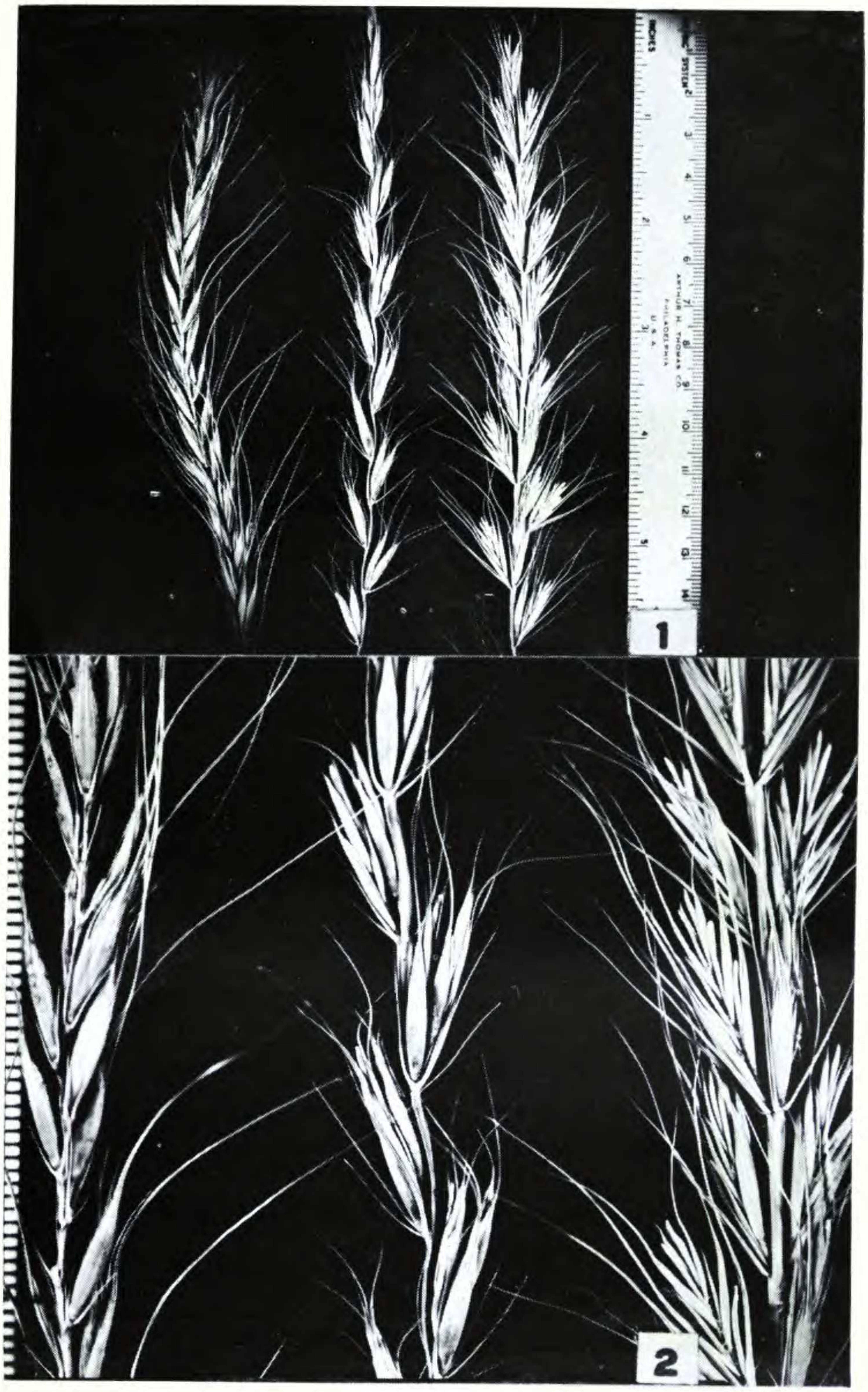


Fig. 1. (left to right) *E. diversiglumis* 2476; *E. Svensonii* 2527; *E. canadensis* var. *interruptus* 1041. Fig. 2. Same as fig. 1, but greater magnification.

Scale shown in millimeters

Plate 1343.

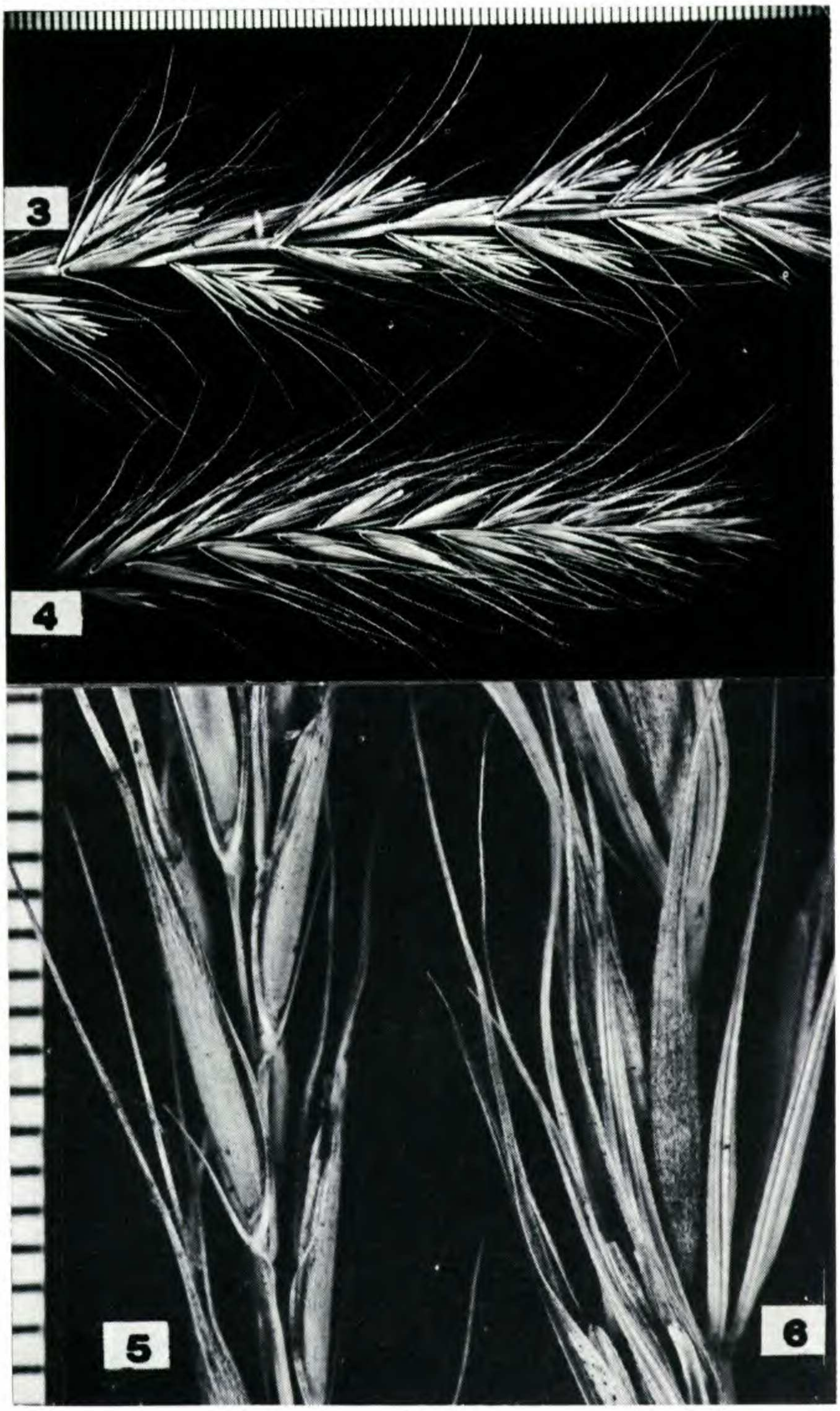
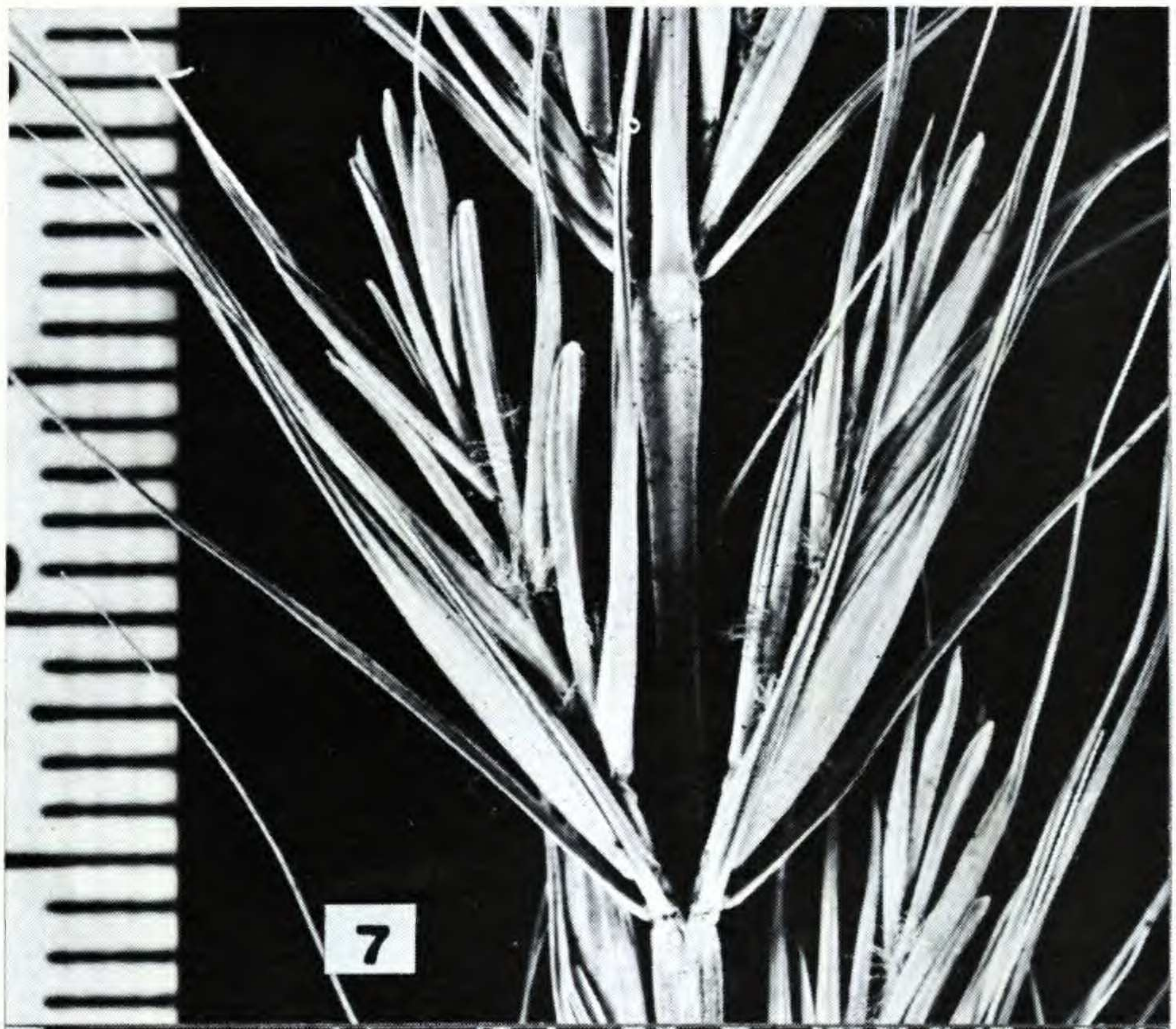


Fig. 3. *E. canadensis* var. *interruptus* 1041. Fig. 4. *E. canadensis* var. *brachystachys* 1028. Fig. 5. *E. diversiglumis* 2328. Fig. 6. *E. canadensis* var. *canadensis* 2300.

Scale shown in millimeters

Plate 1344.



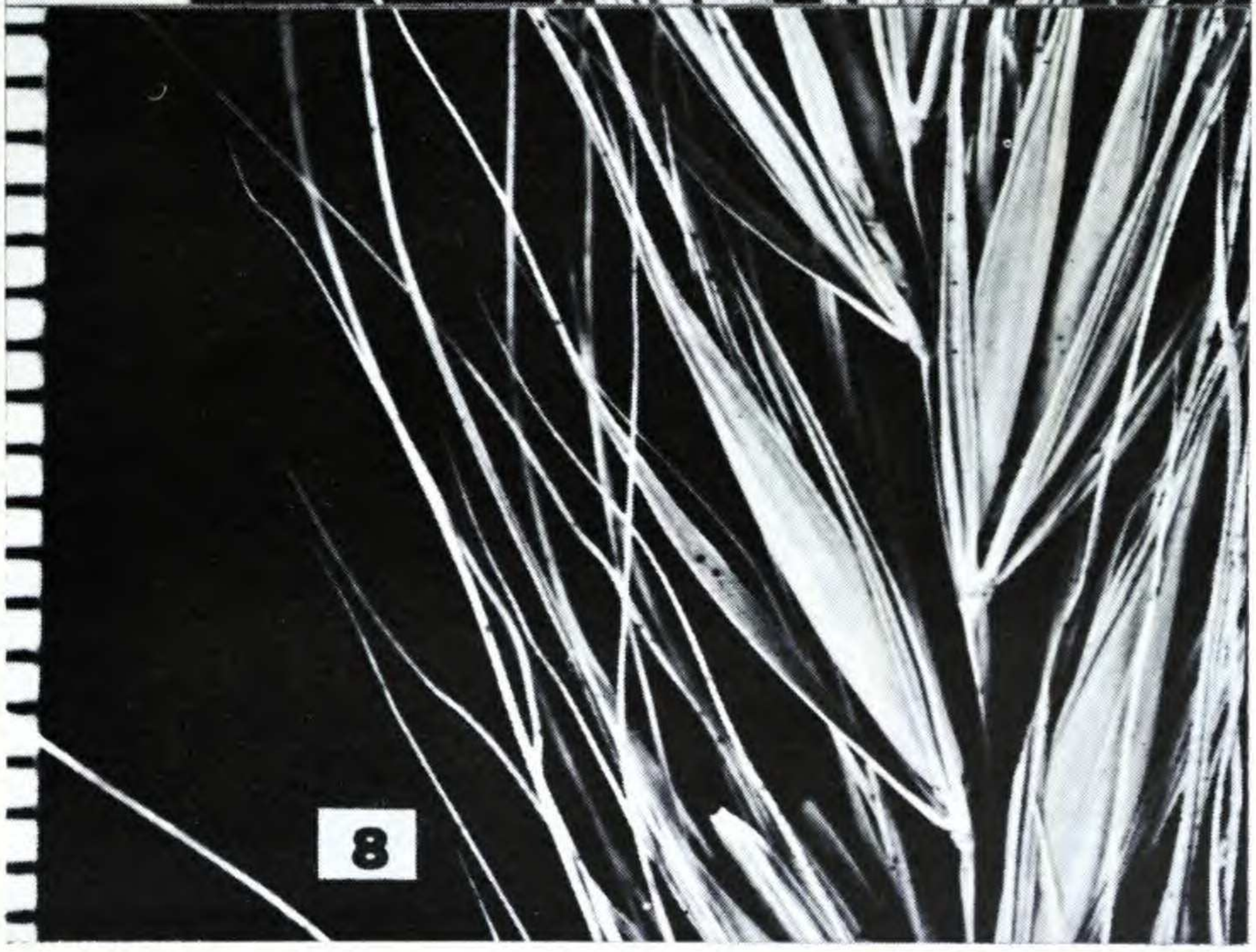
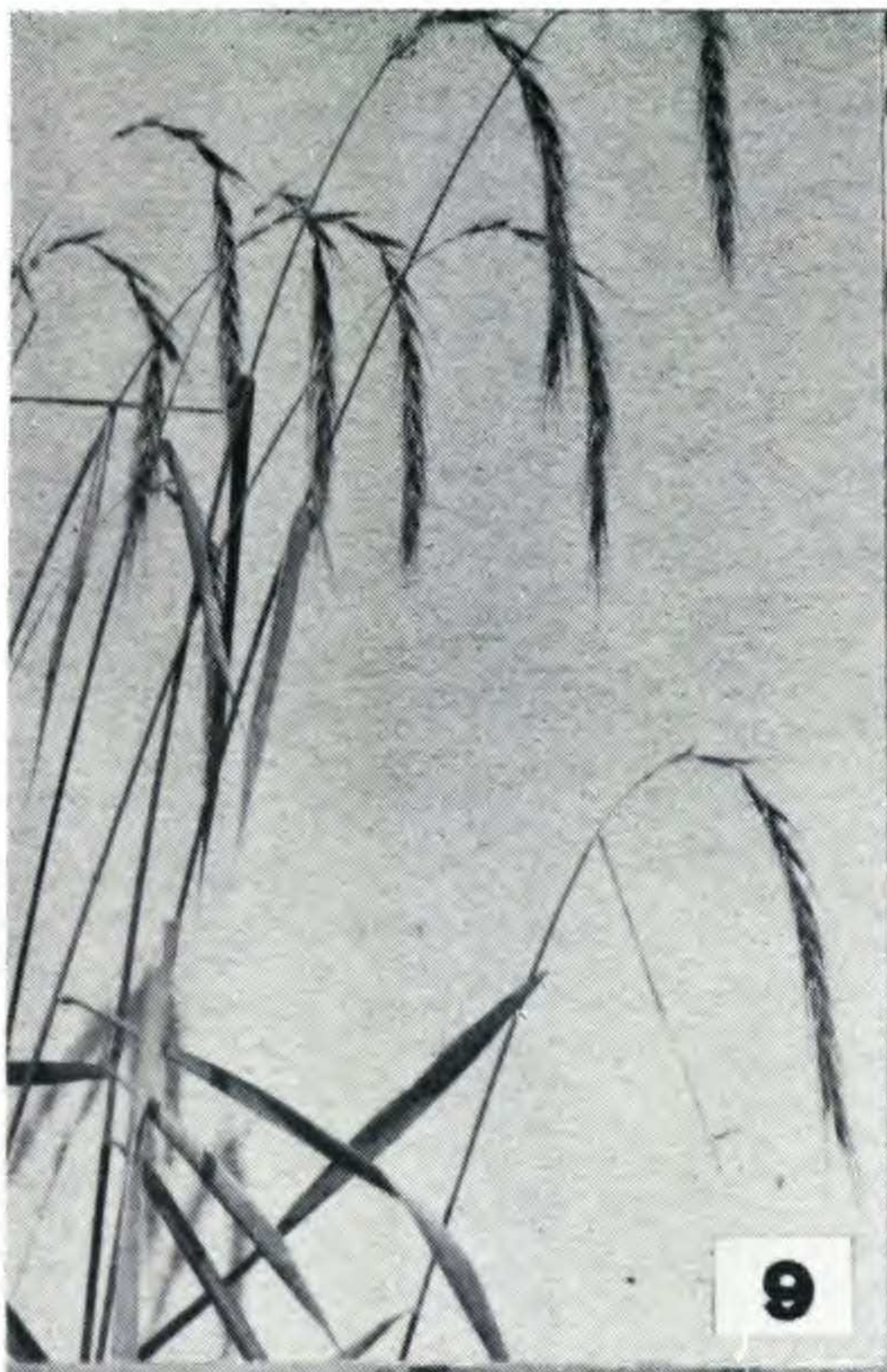


Fig. 7. *E. canadensis* var. *interruptus* 1041. Fig. 8. *E. canadensis* var. *brachystachys* 1028.

Scale shown in millimeters

Plate 1345.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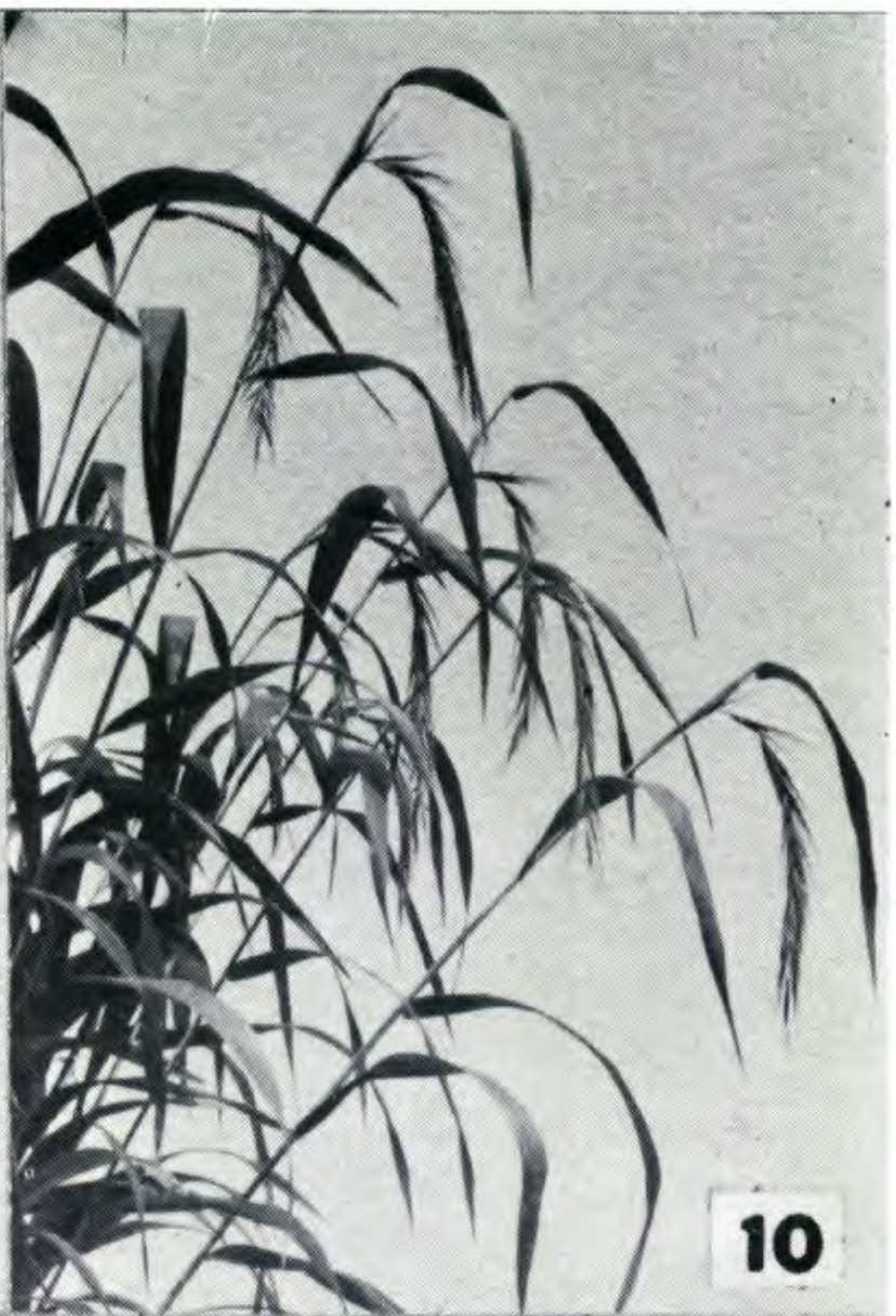
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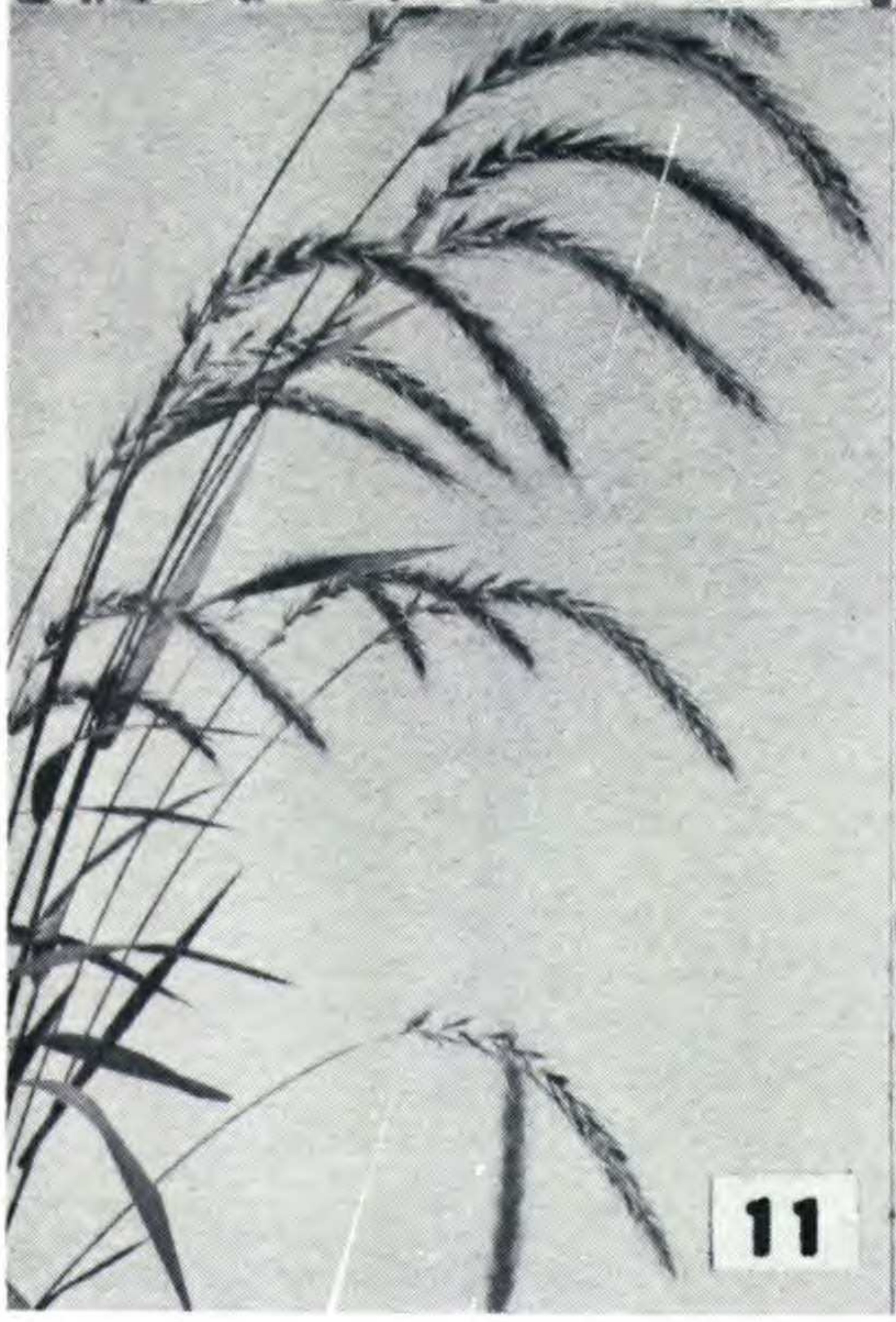
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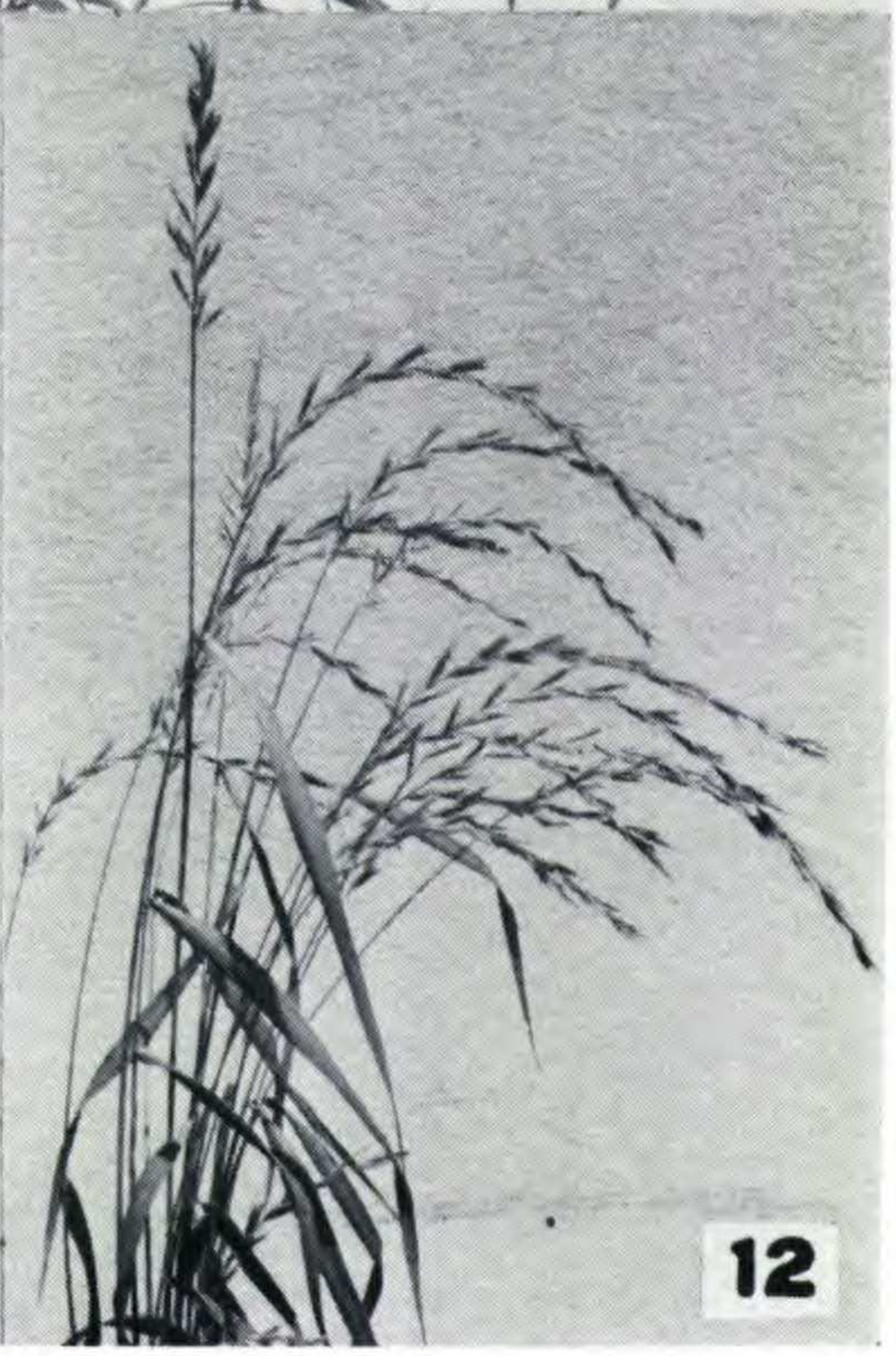

12

Fig. 9. *E. diversiglumis* 2508. Fig. 10. *E. Wiegandii* 2522. Fig. 11. *E. canadensis* var. *canadensis* 2300. Fig. 12. *E. Svensonii* 2527.

Plate 1346.

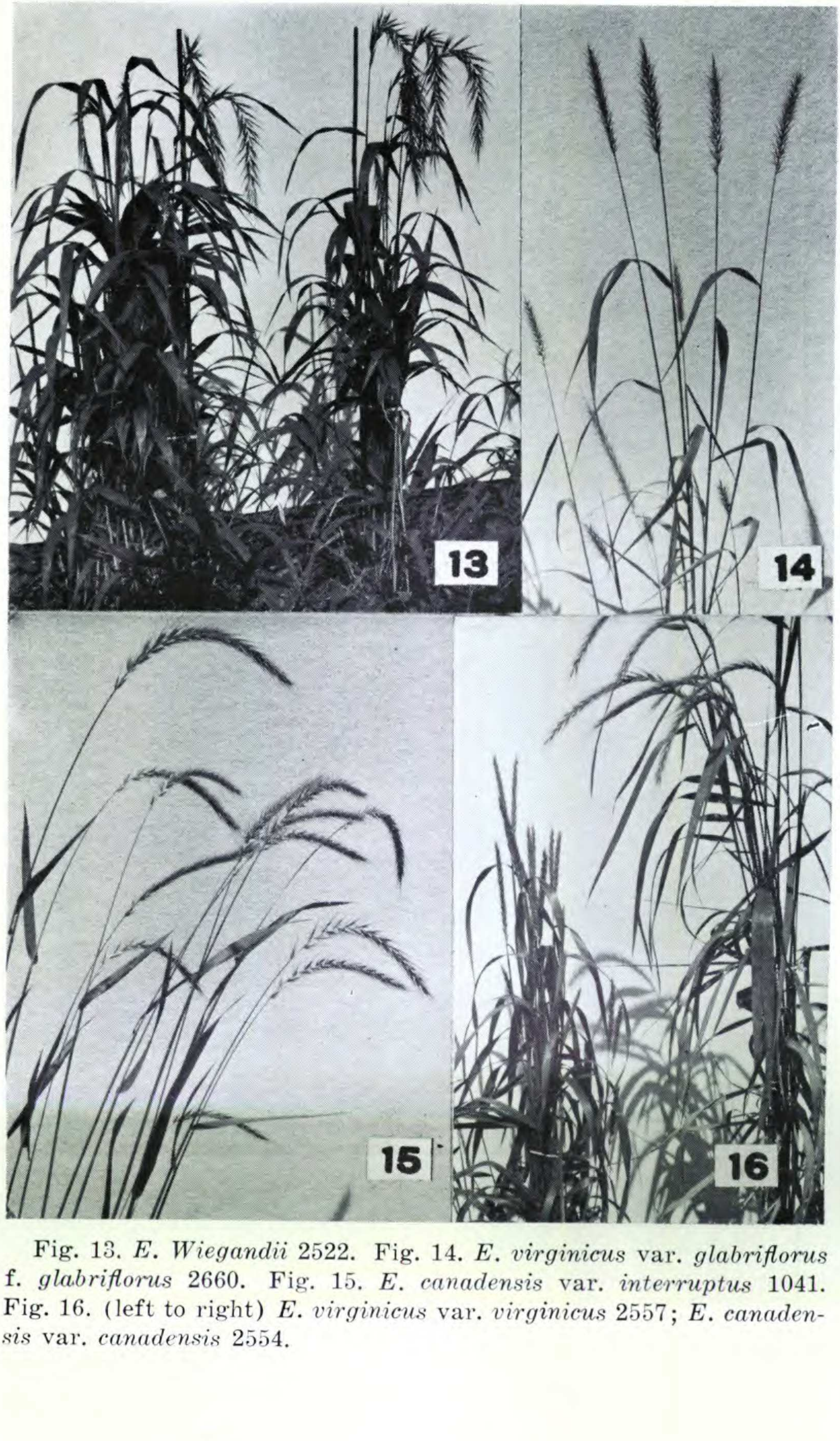
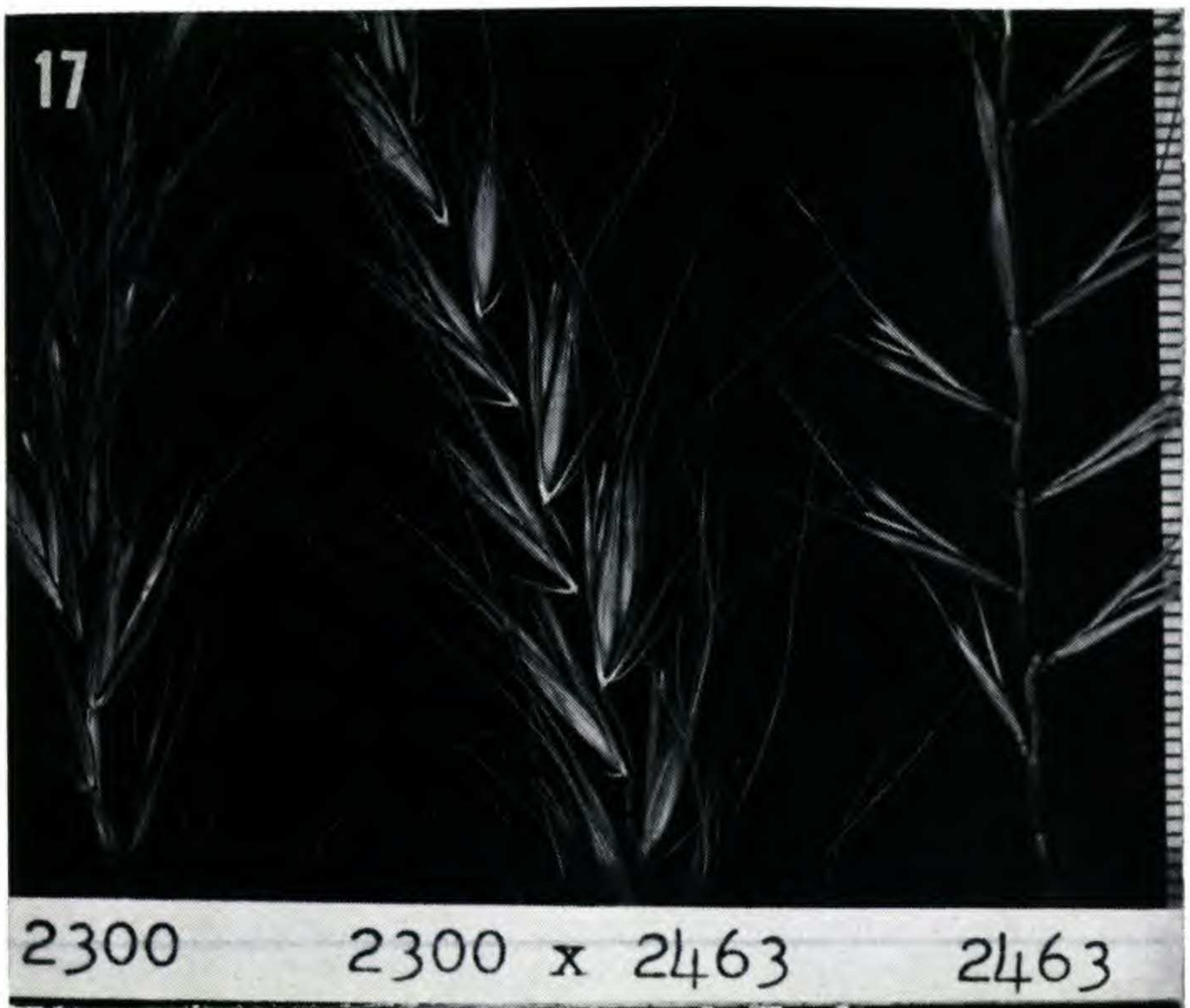


Fig. 13. *E. Wiegandii* 2522. Fig. 14. *E. virginicus* var. *glabriflorus* f. *glabriflorus* 2660. Fig. 15. *E. canadensis* var. *interruptus* 1041. Fig. 16. (left to right) *E. virginicus* var. *virginicus* 2557; *E. canadensis* var. *canadensis* 2554.

Plate 1347.



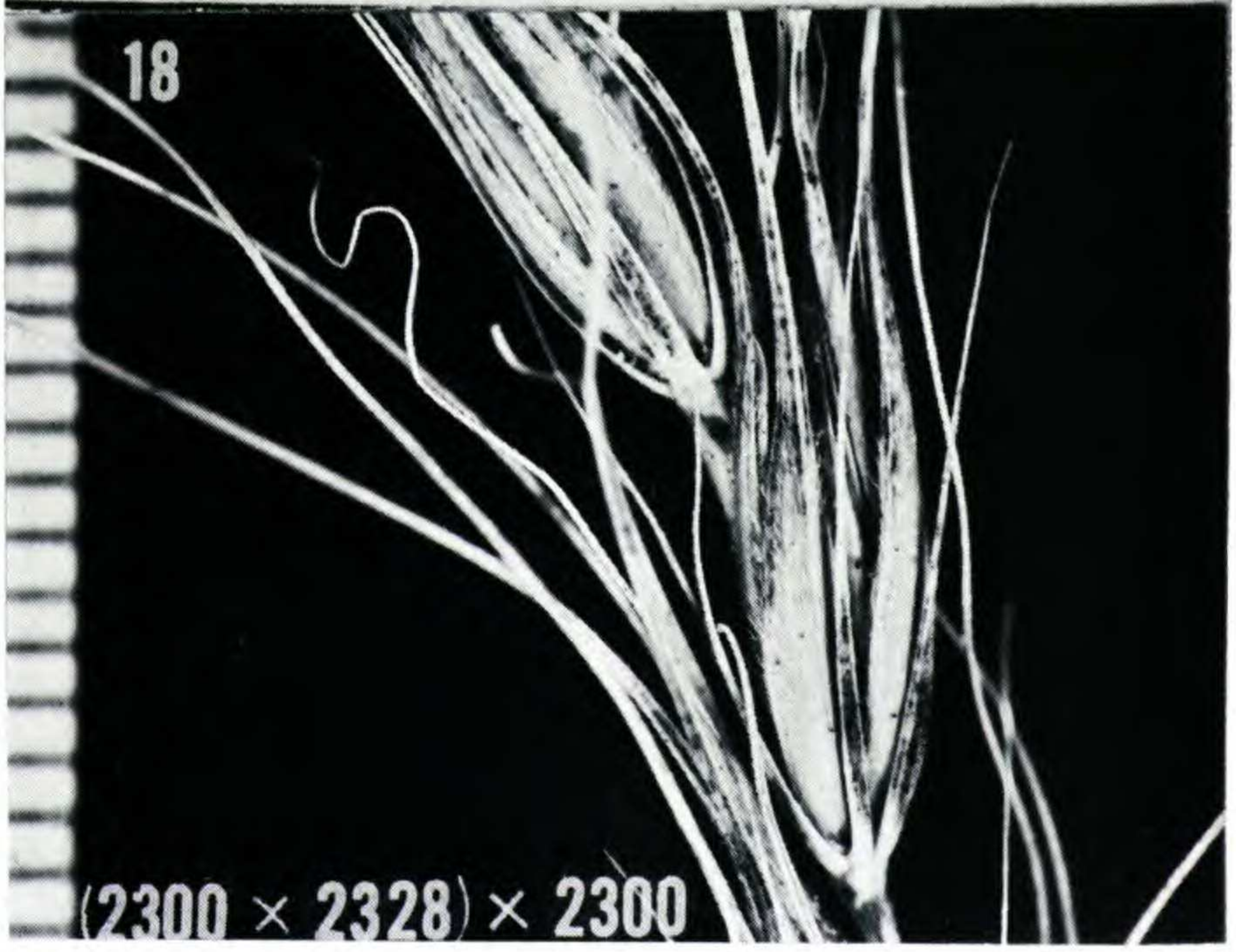
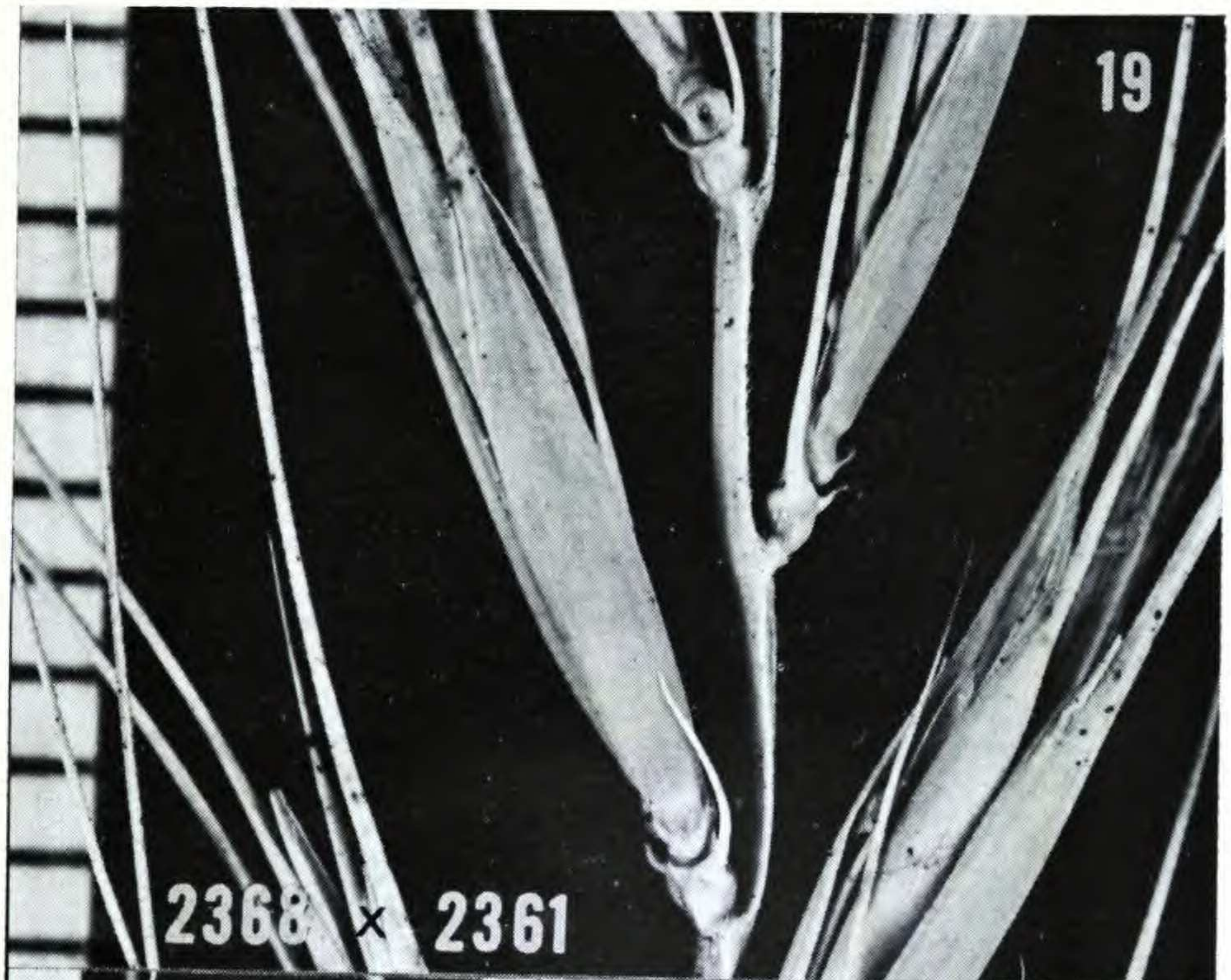


Fig. 17. (left to right) *E. canadensis* var. *canadensis* 2300 (pistillate); experimental F_1; *E. Hystrix* 2463 (staminate). Fig. 18. Backcross of 2300 *(E. canadensis* var. *canadensis)* staminate to experimental hybrid 2300 *(E. canadensis* var. *canadensis)* × 2328 *(E. diversiglumis)*.

Scale shown in millimeters

Plate 1348.



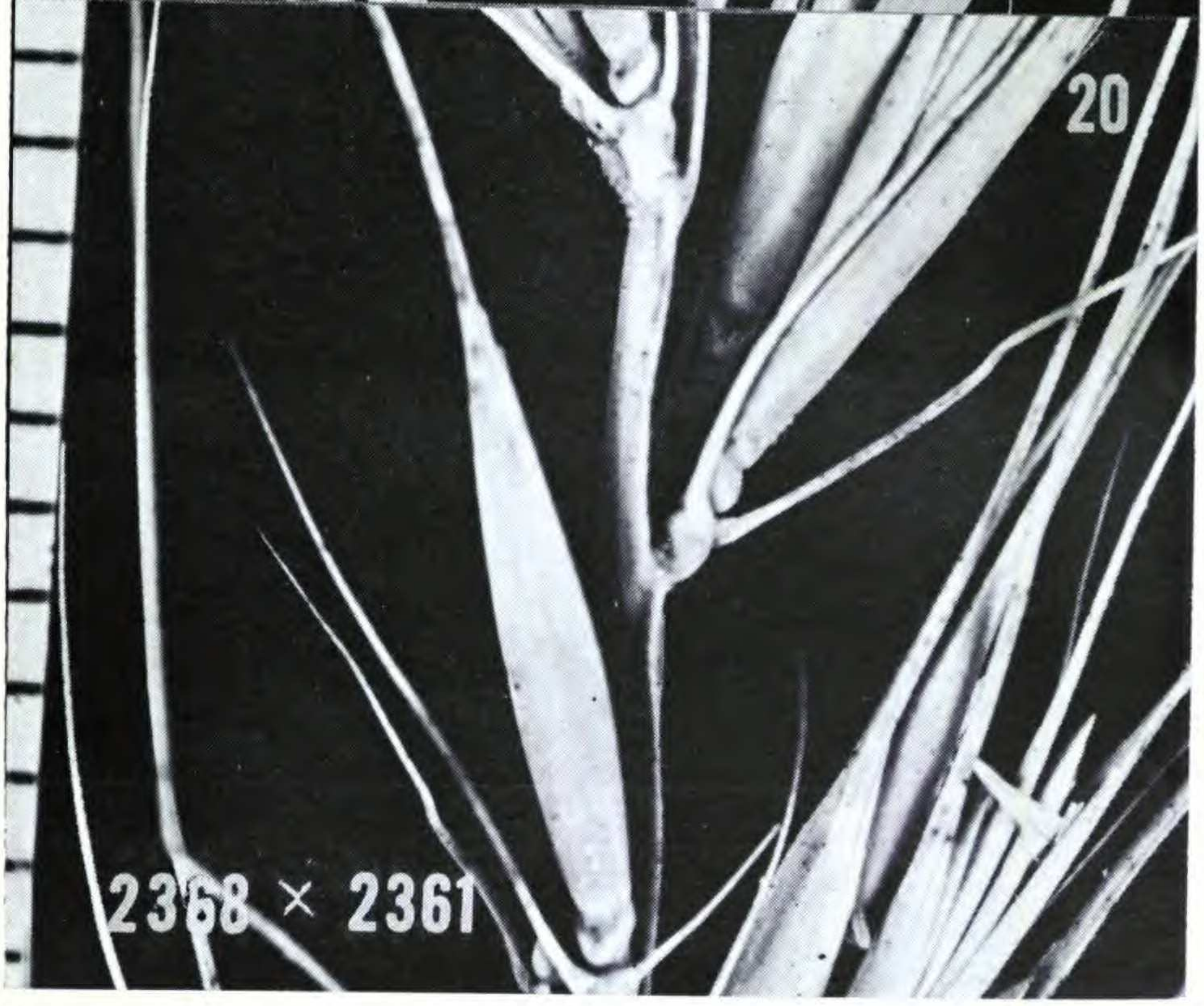


Fig. 19. Experimental cross of 2368 *(E. Hystrix)* × 2361 *(E. diversiglumis.)* Fig. 20. Another region of the same spike as fig. 19. Scale shown in millimeters

Plate 1349.

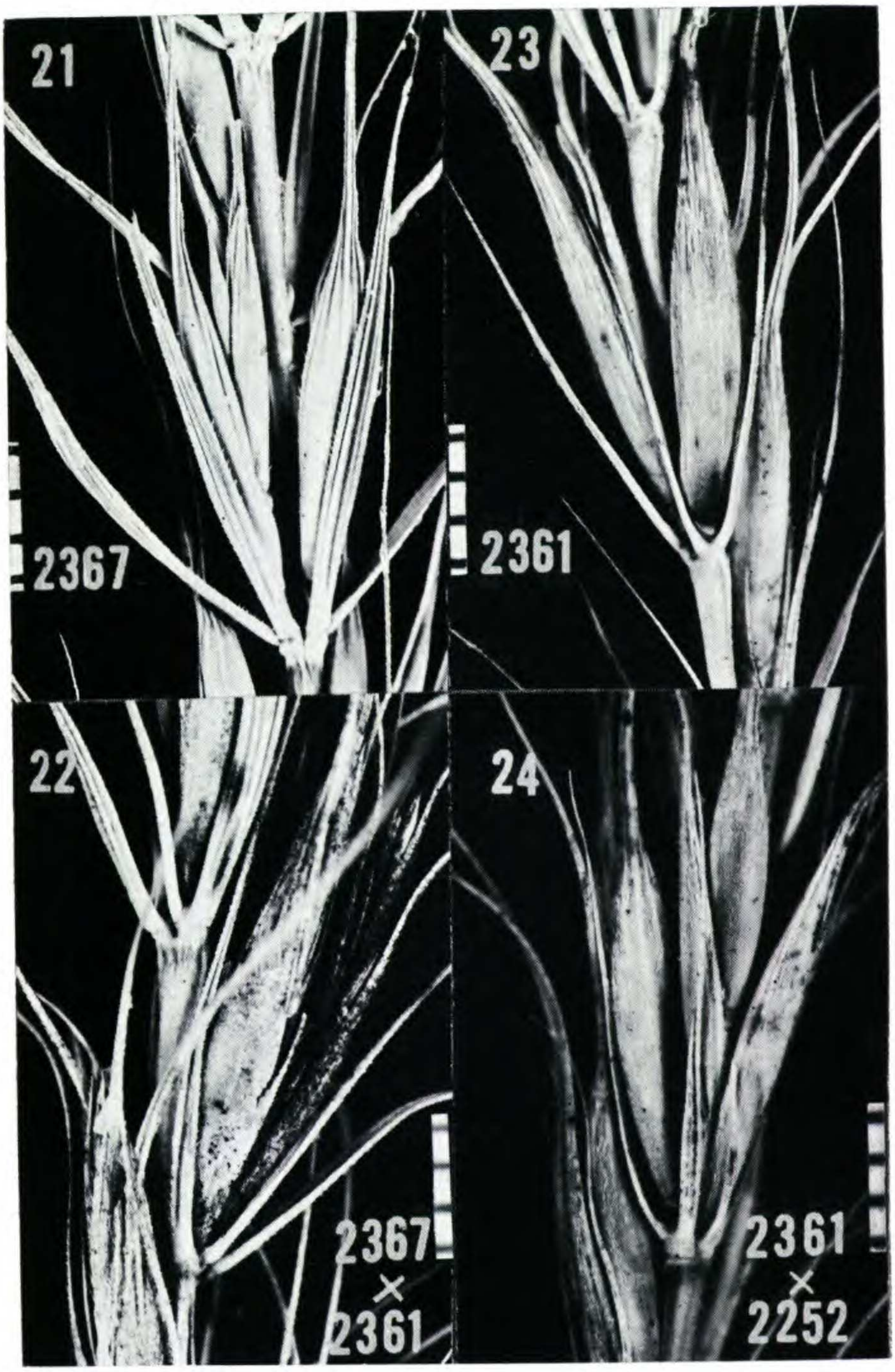
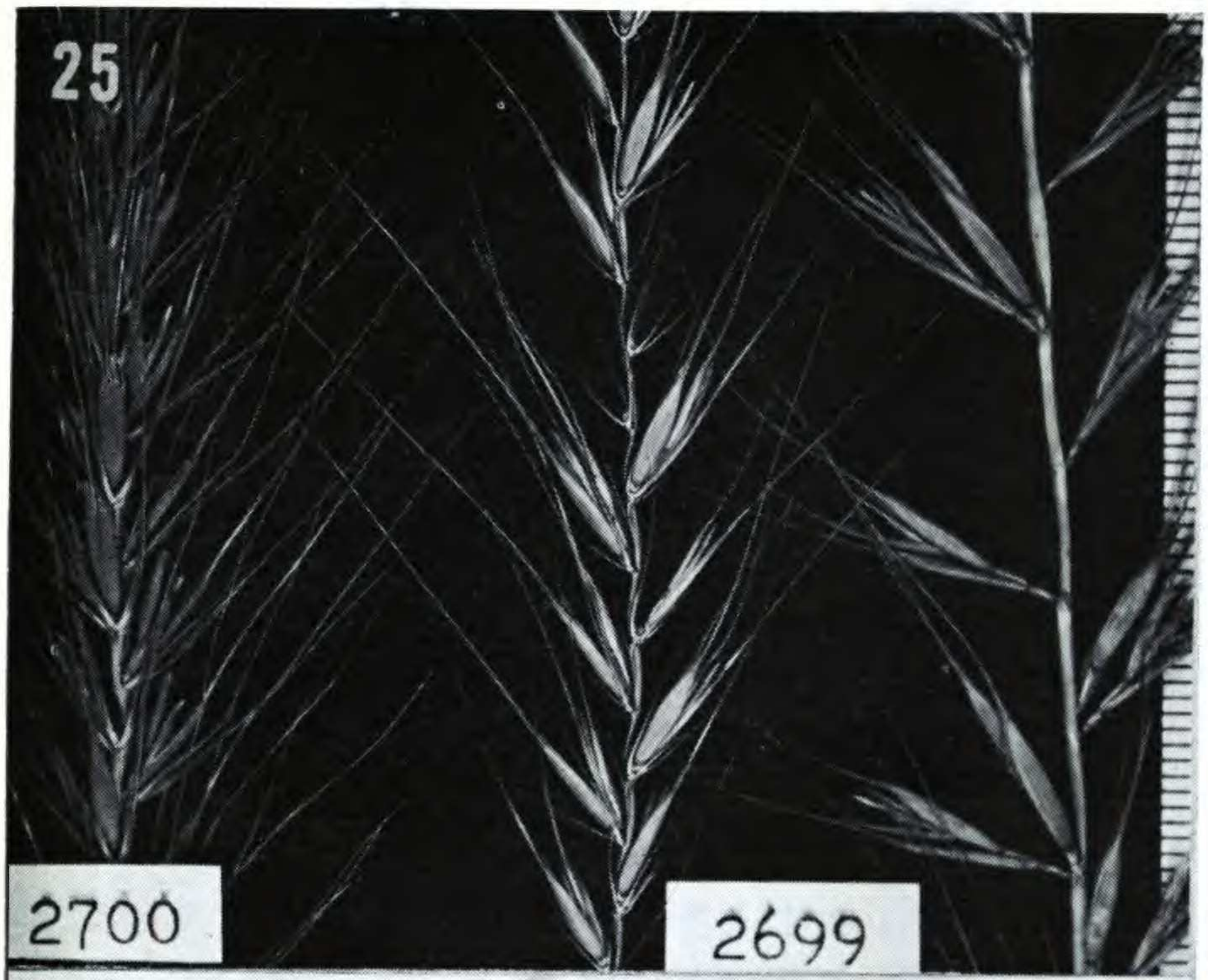


Fig. 21. *E. riparius* 2367. Fig. 22. Experimental cross of 2367 *(E. riparius)* × 2361. *(E. diversiglumis)*. Fig. 23. *E. diversiglumis* 2361. Fig. 24. experimental cross of 2361 *(E. diversiglumis)* × 2252 *(E. canadensis* var. *canadensis)*.

Scale shown in millimeters

Plate 1350.



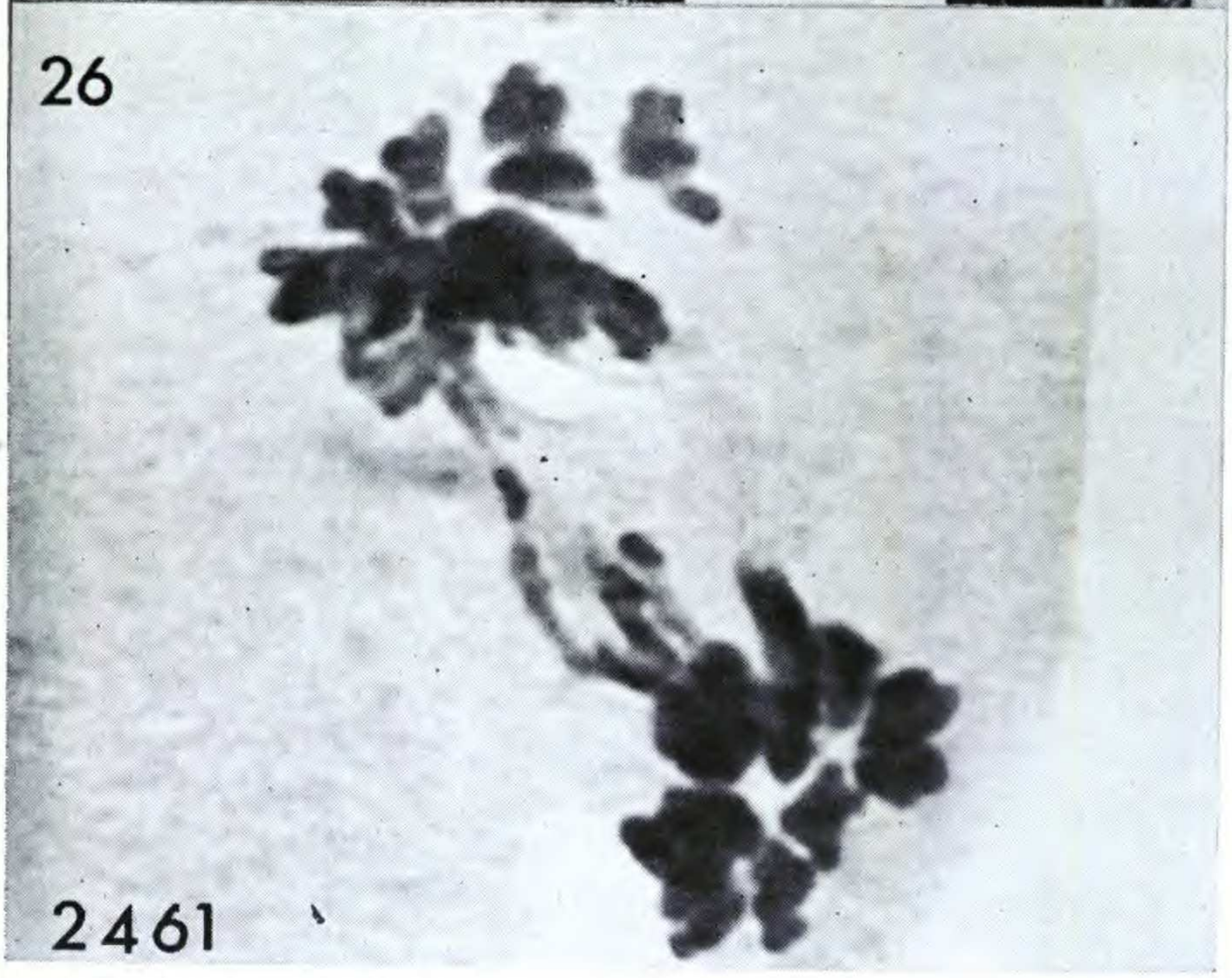


Fig. 25. *E. villosus* 2700; two spikes of the same population of *E. Hystrix* 2699. Scale shown in millimeters. Fig. 26. Pollen-mother-cell of *E. diversiglumis* 2461, late first meiotic anaphase showing bridges.

GENETIC RELATIONSHIPS

In testing the hypothesis that *E. Hystrix* and *E. canadensis* var. *canadensis* might cross to give rise to hybrid populations with setaceous glumes in Minnesota (Booher and Tryon 1948), experimental crosses between representative strains were made in order to learn the extent of the genetic barriers existing between them. However, since populations of *Elymus* with setaceous glumes may be found also in the following cases, similar experimental crosses were made with the hope of obtaining data indicative of the origin of the taxa involved: — *E. canadensis* var. *interruptus* in Texas, *E. Svensonii* in Tennessee and *E. virginicus* var. *glabriflorus* in Illinois.

METHODS. Since none of the strains employed was self-sterile, pistillate parents were emasculated and pollination was effected by dusting the stigmas liberally with pollen collected in cellophane bags that had covered the staminate spikes.

Results of the crosses are indicated by numbers separated by colons and represent in the following order: — F_1 seedlings obtained, seeds obtained from the cross, florets emasculated. Numbers in square brackets indicate original seedlings obtained in contrast to preceding number of surviving mature plants. In cases where no square brackets are used, all seedlings grew to mature plants. Two numbers alone indicate: — mature plants: seeds planted.

Cytological data, when given, are based on the examination of at least 50 pollen-mother-cells (p.m.c.'s) in the stages reported. Chiasma frequencies represent average chiasmata per bivalent chromosome at diakinesis or first meiotic metaphase.

1. Crosses of *E. Hystrix* with *E. canadensis* var. *canadensis*.

On the edge of mixed woodlands in the Brainerd-Mille Lacs Lake area, fertile specimens have been collected that have the general appearance of var. *canadensis* but which possess glumes reduced in width or length and yet not identifiable as setaceous. With the thought that such strains might be introgressants of *E. Hystrix* into var. *canadensis,* crosses between these taxa were attempted. Because of the difficulty in emasculating the readily deciduous florets of *Hystrix,* it was not often possible to use this species as the pistillate parent. The following strains were crossed, all with no success: 2300 (var. *canadensis*), Mille Lacs Lake, × 2368 *(Hystrix)*, Nerstrand Woods (0:90) ; 2300 (var. *canadensis*) × 2306 *(Hystrix)*, Itasca Park (0:104) ; 2669 *(Hystrix)*, Pine Hills — Illinois, × 2300 (var. *canadensis*) (0:100).

In contrast to results with the above strains, a vigorous F_1 was obtained from the cross of 2300 (var. *canadensis*) × 2463 *(Hystrix)* from McCraney Lake woods (14:14:43), even though the reciprocal cross failed (0:46). Figure 17 shows the parents and the F_1. It can be noted that the latter plant has the thin, flattened rachis of *Hystrix,* the hirsute lemmas of var. *canadensis* and the setaceous, unistriated, basally indurated glumes that are obviously intermediate.

Cytological observation of p.m.c.'s of the F_1 above revealed chiasma frequencies of 1.80 as contrasted with 2.00 for 2300 (var. *canadensis*) and 1.99 for 2463 *(Hystrix)*. Roughly 30% of both first and second meiotic divisions in the hybrid exhibited an average of 4 univalent laggards and 2 bridges and yet the young pollen was remarkably free from cytoplasmic extrusions. Nine vigorous hybrid plants flourished while surrounded by parental strains in an outdoor plot for five years but continued to remain sterile. Consequently, formation of introgressants from parental backcrossing to the hybrid appears to be precluded.

Still further evidence of the existence of strong genetic barriers between populations of the above taxa is revealed in the failure of a cross of strains from the Pine Hills woodland of southern Illinois: 2669 *(E. Hystrix)* × 2659 (var. *canadensis)* (0:84) and the reciprocal (0:91).

2. Crosses of *E. diversiglumis* with *E. Hystrix*

A cross between 2316 *(diversiglumis)* from Itasca Park and 2513 *(Hystrix)* from Gull Lake was a failure (0:5:98) as was the reciprocal (0:6:104). A similar strain 2317 *(diversiglumis)* from Itasca Park crossed reciprocally with 2463 *(Hystrix)* from McCraney Lake likewise was a failure (0:96), (0:32). Employing 2368 *(Hystrix)* from Nerstrand Woods in a reciprocal cross with 2501 *(diversiglumis)* from Itasca Park still resulted in failure (0:104), (0:112). However, the use of 2361 *(diversiglumis)* from Gull Lake as the staminate parent in a cross with 2368 *(Hystrix)* produced a vigorous F_1 plant (1:3:222). This plant strongly resembled *Hystrix* with a few filiform glumes (figs. 19 and 20) and revealed a chiasma frequency of 1.85. In the examination of ca. 500 pollen-mother-cells, 10% showed univalent laggards, extrusions and bridges. Sixteen seeds produced an F_2 of 4 plants, entirely sterile, although still resembling the *Hystrix* parent.

3. Crosses of *E. diversiglumis* with *E. canadensis* var. *canadensis*

Striking success attended a cross of a very vigorous 2461 *(diversiglumis)* from McCraney Lake with 2523 (var. *canadensis*) from Mille Lacs Lake (13[20]:20:46). Of the surviving F_1, half were fertile *diversiglumis* and half were sterile var. *canadensis*. Since 2461 *(diversiglumis)* showed some meiotic irregularities (fig. 26), it was heterozygous, probably for genes from var. *canadensis* acquired through previous natural hybridity. In this case the above experimental cross represented a backcross, a fact that would explain the segregation of progeny in the F_1. The reciprocal cross 2523 × 2461 (6:37:67) produced a fertile F_1 resembling *diversiglumis* but with equal glumes 0.3 mm wide and ribbed to the indurated base. Still further evidence of the heterozygosity of this same 2461 *(diversiglumis)* is the fact that another cross with 2300 (var. *canadensis*) from Mille Lacs Lake used as the pistillate parent resulted in two F_1 plants (2:3:66), one essentially like var. *canadensis* and the other a vigorous *diversiglumis* with intermediate glumes. However, the latter segregate yielded only 6 seeds out of 380 florets.

The employment of another strain of *diversiglumis*, less vigorous but free from meiotic irregularities, demonstrated more strikingly how partially fertile strains, intermediate with var. *canadensis*, might arise through introgression. In a cross of 2300 (var. *canadensis*) Mille Lacs Lake with 2328 *(diversiglumis)* Itasca Park, the F_1 (2[3]:24:80) was definitely intermediate with respect to glumes and paleas, but revealed laggards, bridges and extrusions in 30% of the 100 p.m.c.'s examined and a seed set of only 15%. The backcross made with 2300 (var. *canadensis*) pollen produced a vigorous plant (1:1:32), still possessing intermediate glumes but yielding a higher seed set of 25%. This experimental backcross closely resembles natural populations exhibiting a similar degree of intermediate morphology and partial sterility (2327, 2340, 2514) that have been collected in the Itasca Park and Round Lake areas.

The use of an allopatric strain of var. *canadensis* from Vermont demonstrated a lower level of genetic barriers with respect to the vigorous 2361 *(diversiglumis)* from Itasca Park. This cross of 2361 with 2252 (var. *canadensis*) from Vermont (figs. 23 and 24) yielded an F_1 (20:32:76) that had narrow, but rarely setaceous glumes and was 40% fertile. The backcross made with 2361 *(diversiglumis)* pollen produced a rather weak, sterile F_1.

4. Cross of *E. diversiglumis* with *E. riparius*

Although not frequently encountered in the Great Lakes area, *E. riparius* is a species with distinctly terete and indurated bases to the glumes, a character which might contribute to setaceousness of the glumes of sympatric species with which it might hybridize. However, the F_1 (4:26:98) of the cross of 2367 *(riparius)* from Nerstrand Woods with 2361 *(diversiglumis)* from Itasca Park (figs. 21 and 22) was completely sterile.

5. Crosses of *E. Wiegandii* with *E. canadensis* var. *canadensis*

All attempts at hybridization between strains of both *E. Wiegandii* and var. *canadensis* met consistently with failure: — 2522 *(Wiegandii)* Mille Lacs area with 2519 (var. *canadensis*) Mille Lacs Lake and reciprocal (0:27), (0:26); 2522 *(Wiegandii)* with 2317 (var. *canadensis)* Itasca Park and reciprocal (0:20), (0:29); 2511 (var. *canadensis*) Round Lake with 2522 *(Wiegandii)* (0:54); 2550 (var. *canadensis*) Lake Michigan shore with 2522 *(Wiegandii)* (0[8]:8:57); 2519 (var. *canadensis*) Mille Lacs Lake with 2538 *(Wiegandii)* from Itasca Park (0:31); 2300 (var. *canadensis*) Mille Lacs Lake with 2517 *(Wiegandii)* Mille Lacs Lake (0:58); 2522 *(Wiegandii)* Mille Lacs with 2523 (var. *canadensis*) Mille Lacs (0[4]:20:148); 2550 (var. *canadensis*) Lake Michigan shore with 2522 *(Wiegandii)* Mille Lacs (0[2]:8:57).

In the cases listed in which a few F_1 seedlings developed and then died, the failure was associated with an intense formation of anthocyanin pigment.

The above experimental data certainly substantiate the recognition of *E. Wiegandii* as a species very distinct from *E. canadensis* var. *canadensis.*

6. Crosses of *E. Wiegandii* with *E. Wiegandii*

Certain strains of *E. Wiegandii* from the Mille Lacs Lake area (2499, 2517, 2522) exhibited lagging univalents, bridges and a chiasma frequency of 1.90 in 300 p.m.c.'s examined. Yet fertility in terms of percentage of seeds was not greatly reduced. Since the above data suggested the existence of genetic barriers between populations in central Minnesota, experimental crosses between the following sympatric strains were made: — 2502 *(Wiegandii)* Brainerd crossed with 2522 *(Wiegandii)* Mille Lacs (32:32:70) and the reciprocal (36:36:70). The complete fertility of the F_1 is indicative of the taxonomic identity of the strains.

By way of comparison with the sympatric cross, an allopatric cross was made between 2438 *(Wiegandii)* from Itasca Park and 2536 *(Wiegandii)* from Mattapedia, Quebec (20:21:42) and the reciprocal (14:14:28). Examination of the pollen-mother-cells revealed chiasma frequencies ranging from 1.70 to 2.00 and irregularities in meiosis were rare. Yet, in contrast to the sympatric crosses, the Minnesota with Quebec crosses were largely sterile. A similar correlation between geographic range and genetic barriers has been found in crosses of *E. canadensis* var. *canadensis* from Vermont with strains from Minnesota. For example, in the cross of 2252 (var. *canadensis*) from Vermont with 2300 (var. *canadensis*) from Mille Lacs, no seeds were obtained (0:212). With respect to the implied limits of genetic barriers between strains in the above tests, the strains of *Wiegandii* are more closely related to each other than are the interregional strains of var. *canadensis*.

7. Crosses of *E. Wiegandii* with *E. diversiglumis*

In broadly sympatric populations of *E. diversiglumis* and *E. Wiegandii*, both species may exhibit characters in common; i.e., very drooping spikes, glaucous, dark green adaxially pilose leaves and varying degrees of setaceous glumes. Although other characters may be found to separate these species (cf. key), experimental crosses were made to test the possibility of natural interspecific hybridity. As can be seen from the following data, however, all such crosses were failures: 2522 *(Wiegandii)* Mille Lacs Lake with 2328 *(diversiglumis)* Itasca Park (0:86) and reciprocal (0:40), 2361 *(diversiglumis)* Itasca Park with 2517 *(Wiegandii)* Mille Lacs Lake (0:70), 2514 *(diversiglumis)* Gull Lake with 2517 *(Wiegandii)* Mille Lacs Lake (0:58), 2438 *(Wiegandii)* Itasca Park with 2328 *(diversiglumis)* Itasca Park (0:32).

In a cross of 2355 *(diversiglumis)* from Cotton Lake with 2522 *(Wiegandii)*, 7 seedlings were obtained (7:7:40). In the course of a month, however, an intense anthocyanin pigmentation developed in all plants and death ensued after two months. A similar barrier was noted above in a cross of *E. Wiegandii* and *E. canadensis* var. *canadensis*.

8. Crosses of *E. Svensonii* with *E. Hystrix*

Since the Tennessee endemic *E. Svensonii* resembles *E. Hystrix* to some extent, it seemed logical to test the relationship of these species, again by means of artificial hybridization. The vigorous strain 2368 of *Hystrix* from Nerstrand Woods, Minnesota was employed in making reciprocal crosses. The cross with pistillate *Hystrix* resulted in a vigorous, intermediate, partly fertile F_1 (3:4:24). These plants were still surviving three years later in outdoor plots. The F_2 of three plants (3:27) segregated as follows: a sterile, glaucous *Hystrix*, a partially fertile, green *Hystrix* and a fertile intermediate. The latter segregate was still vigorous, though largely sterile, after five years in an outdoor plot. Chiasma frequencies in the intermediate member of the F_2 were 1.90 compared to 2.00 for both parents. Pollen of this hybrid appeared normal. A few seeds from the first year plants produced 6 plants (6:48) all resembling *Hystrix*. These F_3 segregates were sterile.

The reciprocal cross (i.e., with *Svensonii* as the pistillate parent) produced a vigorous but largely sterile F_1 (9:16:22) which resembled a *Hystrix* with adpressed instead of spreading spikelets at maturity. The two seeds obtained produced an F_2 (2:58) that resembled a glumeless *Hystrix* like the staminate parent but possessed reflexed awns and glaucous foliage like the pistillate parent. Ten F_3 plants resembled *Hystrix* very closely, were intensely glaucous and mostly fertile, although they remained in a vegetative state for the first year.

9. Crosses of *S. Svensonii* with *E. canadensis* var. *interruptus*

Since the endemic *Svensonii* has been confused with var. *interruptus* (Hitchcock and Chase 1950), crosses between these taxa were made to determine the degree of possible genetic relationship. The cross of 1041 (var. *interruptus*) from Texas with staminate 2527 *(Svensonii)* produced a vigorous, intermediate F_1 (9[11]:33:90) which was still thriving after five years in the field. The F_2 consisted of 8 vigorous plants (8[11]:18): — one fertile var. *interruptus*, two fertile *Svensonii* and five partly fertile intermediates. The latter forms had spikes with slightly sinuous rachises, widely separated nodes (an *interruptus* character), glaucous foliage and very setaceous glumes (*Svensonii* features). The chiasma frequency of the intermediates was 1.87. More than 50% of the p.m.c.'s examined had bridges and univalent laggards, in contrast to normal meioses in the parents. The four seeds obtained from the F_2 did not germinate.

The cross made with *Svensonii* as the pistillate parent also produced a vigorous F_1 (32[37]:96:293) and again intermediate in appearance. The F_2 (8:36:96) segregated equally to give partly fertile intermediates and sterile, vegetable plants. The single F_3 plant (1:8:25) obtained was stunted and sterile. The chiasma frequency of the F_1 was 1.86, very close to that of the reciprocal cross. In some 800 p.m.c.'s examined, irregularities proved to be relatively infrequent.

10. Crosses of *E. Svensonii* with *E. diversiglumis*

Crosses with 2428 *(diversiglumis)* from Itasca Park were failures (0:108), reciprocal (0:125). Similar crosses with 2355 *(diversiglumis)* from Cotton Lake, Minnesota were likewise failures (0:158), reciprocal (0:110).

11. Crosses of *E. Svensonii* with *E. virginicus* var. *virginicus*

Since it has been demonstrated that various strains of *E. virginicus* var. *virginicus* have genes in common with many other species (Stebbins and Snyder 1956, Church 1959), reciprocal crosses were made with *Svensonii* in order to probe further into the genetic background of this Tennessee endemic. The cross with pistillate 2542 (var. *virginicus*) from Texas, produced a husky, partly fertile, intermediate F_1 (27:29:129). The F_2 (23:38) was entirely glaucous like the staminate 2527 *(Svensonii)* parent, but segregated into several categories as to width of glumes. Most of the latter forms were sterile except for one with glumes only slightly wider than those of *Svensonii* and a seed set of 15%. Cytological studies of the p.m.c.'s in the intermediates of the F_1 revealed a chiasma frequency of 1.82. Laggards and extrusions in 50% of the division stages appeared to be the cause of much of the shrivelled pollen.

The reciprocal cross (18:19:150) produced intermediate plants with glumes much nearer to var. *virginicus* than to *Svensonii* in form and width. The few seeds obtained failed to germinate (0:14). Chiasma frequency was 1.84 and laggards, bridges and extrusions were common in all later stages of meiosis.

A cross with 2641 (var. *virginicus*) from Michigan employed as the staminate parent produced only a single, stunted sterile F_1 plant (1[4]:6:116).

12. Crosses of *E. canadensis* var. *interruptus* with *E. diversiglumis*

Although the taxonomic confusion between var. *interruptus* and *diversiglumis* has been clarified earlier in this paper, it is of interest to present now the degree of genetic barriers between these taxa as based on the data from experimental hybrids. The cross of 1041 (var. *interruptus*) from Llano County, Texas with 2461 *(diversiglumis)* from McCraney Lake, Minnesota as the pistillate parent was relatively successful (17[24]:41:268) in the production of a rather intermediate F_1 which, however, was completely sterile. Chiasma frequency was 1.83 and in all stages of meiosis examined, ca. 40% of the p.m.c.'c revealed laggards, bridges and extrusions. The cross made with 1041 (var. *interruptus*) as the pistillate parent again resulted in a completely sterile F_1 (3:3:70) with narrow glumes and hirsute lemmas. A cross attempted with 2450 *(diversiglumis)* from Itasca Park, Minnesota as the pistillate parent was a complete failure (0:134).

13. Crosses of *E. canadensis* var. *interruptus* with *E. virginicus* var. *glabriflorus* f. *glabriflorus*

The variety *glabriflorus* of the widespread *E. virginicus* is found mostly below the 40 degree parallel in North America and is distinguished from northern varieties by much longer and thinner glumes. Forms with glabrous or hirsute lemmas are both common (cf. key to species). In Union County, southern Illinois, strains of both forms have been found with very setaceous glumes, the origin of which might be due to introgression from some other southern species. Introgression between *E. canadensis* var. *interruptus* and strains of *E. virginicus* var. *glabriflorus* in Texas has been demonstrated by Brown and Pratt (1960). Hence it was considered appropriate to study the relationships between these two taxa further through experimental hybridization. A cross of 2603 (f. *glabriflorus*) from Illinois as the pistillate parent was made with 1041 (var. *interruptus*) from Texas. The F_1 plants were intermediate in morphology (7:11:81) and had a seed-set of ca. 5%. The F_2 generation of 13 plants segregated as follows:- 3 fertile f. *virginicus*, 4 fertile var. *interruptus* and 6 slightly fertile intermediates. However, the few seeds from the intermediates failed to germinate. The reciprocal cross produced a fairly similar F_2 population of 14 plants that segregated in a similar pattern as follows:- 6 partly fertile f. *virginicus*, one fertile var. *interruptus* and 7 partly fertile intermediates that continued to segregate in the F_3! Although a surprising degree of genetic compatibility was demonstrated between the allopatric strains of this experimental cross, none of the experimental hybrids resemble the aberrant populations of f. *glabriflorus* with setaceous glumes in Union County, Illinois.

14. *Cross* of *E. villosus* with *E. Hystrix*

Although *E. villosus* is quite distinct from other eastern species of *Elymus* in its smaller florets and very compact spikes, the narrow glumes with terete bases suggest that its possible role in the ancestry of natural hybrid populations of *E. virginicus* or *E. Hystrix* should not be overlooked. Furthermore, a natural, bigeneric hybrid between *E. villosus* and *Hordeum jubatum* L. has been described recently from Iowa (Pohl 1966).

A cross between 2520 *(E. villosus)* and sympatric 2521 *(E. Hystrix)* from moist, woodland borders in central Minnesota was a failure (0:94 and reciprocal 0:94).

15. Cross of *E. villosus* with *E. virginicus* f. *glabriflorus*

Again in Union County, Illinois, *E. villosus* grows sympatrically with *E. virginicus* var. *glabriflorus* f. *glabriflorus* or with f. *australis*. Since the strains of *E. villosus* came to anthesis 3 to 4 weeks earlier than those of *E. virginicus* var. *glabriflorus*, experimental crosses were difficult to arrange. However, a cross of pistillate 2652 *(E. virginicus* f. *glabriflorus)* with 2676 *(E. villosus)* produced only one intermediate plant that was stunted and sterile (1:8:21). Another cross of pistillate 2647 (f. *australis*) with 2678 *(E. villosus)* produced seedlings that died after 3 months (3:4:60).

16. Cross of *E. villosus* with *E. virginicus* var *virginicus*

A cross of 2678 *(E. villosus)* and 2600 *(E. virginicus* var. *virginicus)* produced only 5 stunted and sterile F_1 plants (11:16:93). The reciprocal cross produced only inviable seeds (0:6:97).

Within the limits of these data, then, *E. villosus* appears to be quite isolated genetically from both *E. Hystrix* and *E. virginicus*.

DISCUSSION AND SUMMARY

It has been demonstrated that the frequently encountered populations of *Elymus* with very unequal, setaceous glumes in the mixed woodlands of central Minnesota are composed mainly of *E. diversiglumis*, a recently overlooked species. *E. diversiglumis* is quite aggressive in the Minnesota segment of its range, but is distributed sparingly with no obvious phenotypic variations in Wisconsin, Wyoming, the Dakotas and Manitoba. In the disturbed habitats of woodland road embankments, however, forms with wider and longer than typical glumes may be found in vigorous, thick stands that reveal rather low levels of fertility in terms of seed formation (20-50%). Such putative hybrids may exhibit also irregular meioses in the pollen-mother-cells (fig. 26).

Attempts at recreating these aberrant forms of *E. diversiglumis* by crossing sympatric *E. canadensis* var. *canadensis* and *E. Hystrix* resulted mostly in failures. However, a sterile, intermediate F_1 was obtained that resembled *E. Hystrix* with abundant, filiform glumes (fig. 17), but it did not duplicate any natural populations encountered in Minnesota. Furthermore, any close genetic relationship between *E. diversiglumis* and sympatric *E. Hystrix* does not exist in the light of the failure of most of the experimental crosses between these species. On the other hand, the rare, nearly sterile F_1 plant that did appear (figs. 19 and 20) resembled forms of *E. Hystrix* elsewhere in the range. This variant has not yet been found in Minnesota. The F_2 plants were all typically awnless *E. Hystrix* and quite sterile.

Experimental crosses between *E. diversiglumis* and the usually genetically isolated *E. riparius* (figs. 21 and 22) presented intermediate forms whose pattern of origin appears parallel to but not duplicative of that of the aberrant *E. diversiglumis* forms noted above.

It was through crosses and backcrosses of strains of *E. canadensis* var. *canadensis* and *E. diversiglumis* that the production of experimental hybrids that duplicated natural aberrant forms ultimately was made. Populations of *E. diversiglumis* with unusually wide glumes would appear, then, to exhibit introgression from *E. canadensis* var. *canadensis* (fig. 18). The genetic evidence presented indicates that many of the strains of *E. diversiglumis* employed in experimental crosses were already heterozygous for genes from *E. canadensis* var. *canadensis* and that, in effect, backcrosses had been made. Such a pattern of introgressive hybridization would appear to be continuing in central Minnesota. Of further interest is the apparent fact that introgression operates most effectively only with sympatric strains of *E. canadensis* var. *canadensis,* since a strain of the latter from Vermont contributed to the complete sterility of the experimental hybrids (fig. 24).

Since it has been noted that *E. Wiegandii* in some of its characters resembles both *E. diversiglumis* and *E. canaden-*

sis var. *canadensis*, it seemed appropriate to determine the degree of genetic barriers existing between all three sympatric species. The evidence of failure of experimental crosses indicates clearly that not only is *E. Wiegandii* not involved in hybrid complexes of *E. diversiglumis* but that genetic isolation from *E. canadensis* var. *canadensis* also is quite strong. The reduction of *E. Wiegandii* to a variety of *E. canadensis* (Bowden 1964) is not supported by the genetical basis for species integrity presented in this study.

Returning to *E. Hystrix* as a source of genetic control over the appearance of reduced or setaceous glumes in hybridizing populations, the discovery of *E. Svensonii*, with irregular sized, bristly glumes, afforded the opportunity through breeding experiments to probe the genetic relationship of this isolated endemic to not only *E. Hystrix* but to *E. canadensis* var. *interruptus* and *E. diversiglumis*. While clearly isolated genetically from *E. diversiglumis*, it is significant that *E. Svensonii* crossed reciprocally with both *E. Hystrix* and *E. canadensis* var. *interruptus* and that the intermediate F_1 produced a segregating F_2 in all cases, even though the F_3 was sterile. In particular, the fact that the F_2 of *E. Svensonii* and *E. Hystrix* segregated for fertile *E. Hystrix* and partly fertile intermediates would appear to indicate that *E. Hystrix* played a role in the origin of *E. Svensonii*, perhaps in the not too distant geological past.

Various components of *E. virginicus* appear to be able to combine with either *E. Svensonii* or *E. canadensis* var. *interruptus* to produce hybrids with setaceous glumes. When *E. virginicus* var. *virginicus* was crossed with *E. Svensonii*, the F_2 segregated not only for the parents but intermediates as well. In the cross of *E. virginicus* var. *virginicus* f. *virginicus* with *E. canadensis* var. *interruptus*, partly fertile intermediates with more or less setaceous glumes continued to segregate even in the F_3.

In contrast to the demonstrated genetic affinities between *E. Svensonii*, *E. Hystrix* and components of *E. virginicus*, *E. villosus* appears to be quite isolated from *E. Hystrix* and both forms of *E. virginicus* var. *glabriflorus*.

In these studies, it is apparent that the opportunities for the evolution of new taxa with setaceous glumes are more frequent in the relatively southern ranges of species of *Elymus*. A striking instance of the process of speciation, currently operating, will be presented in a second paper involving *E. Hystrix* and *E. virginicus* in southern Illinois.

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